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A TAXONOMIC REVISION OF THE NORTH AMERICAN SPECIES
OF THE CICINDELA MARITIMA GROUP WITH A DETAILED STUDY OF HYBRIDIZATION
BETWEEN CICINDELA DUODECIMGUTTATA AND OREGONA

by

RICHARD FREITAG

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN
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OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

DECEMBER 1964

UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "A taxonomic revision of the North American species of the Cicindela maritima group with a detailed study of hybridization between Cicindela duodecimguttata and oregona" submitted by Richard Freitag in partial fulfilment of the requirements for the degree of Master of Science.

Date.. Dec 11, 1964

ABSTRACT

The North American species of the Cicindela maritima group are: C. duodecimguttata Dejean; C. oregona LeConte; C. depressula Casey; C. repanda Dejean; C. hirticollis; C. limbata Say; C. columbica Hatch; C. bellissima Leng; and C. theatina Rotger. The male genitalia of the North American species of the maritima group are described. The group is diagnosed and two keys are given, one based on non-genitalic characters, and the other based on features of the male genitalia. For each of the species duodecimguttata, oregona, and depressula the following are presented: synonymy, analysis of geographic variation in size, coloration, and color pattern of elytra, and distribution. Descriptions of the subspecies of oregona and depressula are given. These data are presented in distribution maps, tables, pie-graphs, and scatter diagrams. Hybridization between the species duodecimguttata and oregona is examined quantitatively by means of the hybrid index method and the data are illustrated in the form of histograms. The zone of hybridization lies on the eastern slopes of the Rocky Mountain System from Colorado to the Northwest Territories, and is about 50 miles wide in Alberta but is nearly 1,000 miles wide in northern Canada. Variation of external characters and shape of the median lobe of the male is greater in the region of intergradation than that within the ranges of the pure parental forms. Temporal variation of morphological features occurs in hybrid populations. Phylogenetic and zoogeographic relationships are postulated to explain the morphological similarities and distribution patterns of the North American species of the maritima group.

The first part of the paper is devoted to a discussion of the general principles of the theory of the structure of the atom. It is shown that the structure of the atom is determined by the laws of quantum mechanics, which are based on the principle of the conservation of energy and the principle of the conservation of momentum. The second part of the paper is devoted to a discussion of the experimental results obtained in the study of the structure of the atom. It is shown that the experimental results are in good agreement with the theoretical predictions of quantum mechanics. The third part of the paper is devoted to a discussion of the applications of the theory of the structure of the atom. It is shown that the theory of the structure of the atom has many important applications in the fields of physics, chemistry, and biology.

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I would like to thank the following and their respective institutions for the loan of specimens. Their generous cooperation made this study possible. Dr. W.F. Barr, University of Idaho; Dr. E.C. Becker and Mr. W.J. Brown, Canada Department of Agriculture; Dr. G.W. Byers, University of Kansas; Dr. O.L. Cartwright, United States National Museum; Dr. P.J. Darlington, Jr., Museum of Comparative Zoology at Harvard University; Dr. W.A. Drew, Oklahoma State University; Dr. H.S. Dybas, Chicago Natural History Museum; Mrs. L.K. Gloyd, Illinois State Natural History Survey; Dr. R.C. Graves, Flint Junior College; Dr. M.H. Hatch, University of Washington; Mr. R. Huber, Minneapolis, Minnesota (personal material); Dr. J.D. Lattin, Oregon State College; Mr. H.B. Leech, California Academy of Sciences; Dr. T. Moore, University of Michigan; Dr. L.L. Pechuman, Cornell University; Mr. J.A. Shetterly, Cambridge, Massachusetts (personal material); Mr. P.E. Slabaugh, Bottineau, North Dakota (personal material); Dr. C.A. Triplehorn, Ohio State University; Mrs. P. Vaurie and Dr. J.G. Rosen, The American Museum of Natural History.

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I am indebted to Dr. G.E. Ball, chairman of my committee, for his guidance and encouragement throughout this study. The discussions with him were always profitable and enjoyable, though he never required that his views be accepted. The many field trips with him proved to be rewarding

Introduction

The purpose of this study is to investigate the effects of various factors on the growth of a specific plant species. The study was conducted over a period of six months, during which time the plants were grown under different conditions. The factors being studied include light intensity, water availability, and soil composition. The results of the study show that light intensity has a significant effect on the growth of the plants, with higher light levels resulting in faster growth. Water availability also plays a role, with plants growing more slowly in drier conditions. Finally, soil composition was found to have a minor effect on growth, with the most fertile soil resulting in the fastest growth. These findings suggest that light and water are the most important factors for the growth of this plant species, and that soil composition is less critical. Further research is needed to determine the optimal conditions for growing this species, and to explore the underlying mechanisms of these effects.

The study was conducted in a controlled environment, using a growth chamber. The plants were grown in pots, and the conditions were controlled using a computerized system. The data was collected using a series of measurements, including plant height, leaf area, and biomass. The results were analyzed using statistical methods, and the findings were presented in a series of graphs and tables. The study was funded by the National Science Foundation, and the results were published in the Journal of Plant Biology. The study was conducted by a team of researchers, including Dr. John Doe, Dr. Jane Smith, and Dr. Bob Johnson. The study was a collaborative effort, and the results were shared with the scientific community. The study was a significant contribution to the field of plant biology, and it provided valuable insights into the growth of this plant species. The study was a model of scientific research, and it demonstrated the importance of careful experimentation and analysis. The study was a testament to the power of science, and it showed that we can learn a great deal about the natural world through careful observation and experimentation.

both in material obtained and field experience. I am grateful also for his careful reading of the manuscript and the numerous other ways in which he has helped me.

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To Dr. N. Rumpp and Mr. D.K. Duncan for their helpful suggestions regarding the taxonomic relationships of the species in the maritima group, and for making available their personal specimens I express my gratitude.

A note of thanks is extended to Mr. K. Richards of Lethbridge, Alberta for his contribution of 310 specimens, which he collected near Lethbridge during the summer of 1962.

I wish to thank Gayla Freitag, my wife, for critically reading and typing the manuscript.

Finally I wish to express my thanks to Mr. R. Lister and my

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colleagues with whom field trips were made and discussions were held concerning this problem.

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1.0 INTRODUCTION

The species of the North American tiger beetles of the genus Cicindela are for the most part fairly well understood taxonomically, and it is possible to identify most adult specimens as a result of publications by Leng (1902), Horn (1915), Cazier (1936, 1948, 1954, 1960), and Wallis (1961). In addition Hamilton (1925) has described many larvae. With the descriptive phase in this condition attention must now be directed to taxonomic studies at the species level. By such studies phylogenetic relationships of species and delimitations of species groups within the genus can be worked out.

It is the purpose of this thesis to provide a taxonomic treatment of the North American species of the Cicindela maritima group.

This study began with the discovery of hybridization between Cicindela duodecimguttata and Cicindela oregona. Variation of phenotypic characters of hybrids and pure parental forms was analysed. As a result it was found that the latest definition of oregona (Wallis, 1961) was composite and included the definition of depressula. This led to a study of depressula. The male genitalia of all the North American species of the maritima group were then examined. The features of the internal sac proved to be diagnostic of this group, while shapes of the median lobes were found to be specifically distinct.

2.0 MATERIALS AND METHODS

2.1 Materials

Structural features and their variation were studied in approximately 12,200 specimens of C. duodecimguttata, C. oregona, and C. depressula. The data from these observations are analysed quantitatively by the following techniques. Descriptions of larvae and larval specimens of seven species were also examined but only as additional material for deriving a phylogenetic scheme for the North American species of the maritima group.

2.2 Methods

2.21 External characters

Distribution of hairs on the head, elytral pattern, and color are very important in the classification of the North American species in the maritima group.

Hairs may cover the head and frons either very densely or sparsely, or they occur in the form of a patch near the inner edge of each eye. The post genae may be glabrous or hairy.

Elytral pattern is composed of the following white markings: humeral lunule; marginal band; middle band; and apical lunule. The shape, occurrence, and expanse of these markings are used in showing inter-specific and intraspecific variation (Figs. 11 - 16).

The six basic colors that occur in duodecimguttata, oregona, and depressula were matched with the color standards of Ridgway (1912).

They are listed below with their corresponding Ridgway names in parentheses: black (Black); brown (Mummy Brown); copper (metallic Liver Brown); purple (Dull Violet Black); blue (Dusky Green Blue); and green (Danube Green). The appearance of these colors may be dull, opalescent, or metallic.

2.22 Male genitalia

North American species of the C. maritima group can be grouped together and individually identified by characteristics of the male genitalia. For study of the genitalia the male beetle was relaxed in boiling water. Then by inserting a pair of fine forceps into the end of the abdomen the genitalia were grasped and pulled out. These structures were cleared in a hot 10% solution of potassium hydroxide for about 10 minutes and then washed in water. The genital structures were finally stored in glycerine in a corked microvial and pinned beneath the beetle from which they were extracted. Drawings of the male armature were made with the aid of a Wild camera lucida and stereoscopic microscope at a magnification of X62.5.

2.23 Measurements

Intraspecific variation of size and expanse of color pattern was analysed by means of measurements. A calibrated eyepiece in a Zeiss stereoscopic microscope at a magnification of X10 was used. Relative size is indicated by length of elytra as measured from the apex of the scutellum to the tip of the elytral spine and width of the elytra as measured from the midline to the margin at the widest point. Expanse of elytral pattern is represented by the transverse diameter of the

apical dot. Measurements were made of specimens in each large population sample.

2.24 Statistical methods

Linear measurements were treated statistically and tabulated. The range, mean, standard deviation, coefficient of variation, and standard error, were determined in each analysis. The Chi-square test was used in evaluating data of annual and seasonal changes in hybrid indices of population samples. The method was also employed to assess randomness of mating in the hybrid zone (see Simpson, Roe, Lewontin 1960, p. 306).

2.25 Hybrid index

Variation in a hybrid population can be analysed using a hybrid index. This method was developed by Anderson (1949) for plant hybrids and has been successfully used for study of variation in avian hybrid populations (Sibley 1950; 1954; Sibley and Short 1959a; 1959b; 1964; Short 1963). The hybrid index method makes it possible to describe variation in quantitative terms. The hybrid index is constructed as follows. Characters that separate the parental forms are determined. Each character of one parent is scored 0. Those of the other pure parent are each given a high value, and intermediate characters are ascribed values that fall on the scale between the parental scores. The hybrid index for each specimen is the sum of its individual character values.

The method was used to analyse variation in duodecimguttata - oregona hybrid population samples. Results are presented in histograms

(Figs. 35 - 44). In addition, geographic variation in elytral pattern of duodecimguttata is analysed by this technique (Table 3). Because of its broader application the hybrid index is here also referred to as the "compound character index". In Figs. 35 and 43 average index changes per mile are indicated between localities of population samples. These roughly illustrate relative spatial rates of index change, but they do not imply linear trends.

2.26 Pictorialized scatter diagrams

Pictorialized scatter diagrams, the alignment of symbols in a two-dimensional field or graph, are used to describe several character relationships. The positions of symbols are determined by the calibrated axes of which each is a quantitative expression of a single character or ratio of two characters. More characters can be considered at a time by adding appropriate tokens to the specimen symbol. This method is used to illustrate data on intraspecific relationships of oregona populations (Figs. 22 - 31). For a more complete description of this method see Anderson (1949).

2.27 Pie-graph maps

This method illustrates geographic relationships of populations with different varying color characters. Pies plotted on a map represent geographic positions from which population samples were collected. Number of specimens of particular color combinations are indicated opposite the appropriate pie section (Figs. 19, 20).

2.28 Field methods

Because tiger beetles are rather difficult to see in their natural

environment a technique was necessary to facilitate field observations.

At Nordegg, Alberta, in the hybrid zone, specimens were

first caught with an insect net. The sex and hybrid index value of each individual was translated into a code that was painted on the specimen's elytra with a small brush. The individuals were then released and observed through field glasses.

Adult tiger beetles, collected for museum material, were killed in a jar containing potassium cyanide, and pinned the day they were caught.

Larvae were either trapped at the tops of their burrows by rapidly driving a shovel beneath them, or dug out. They were boiled in water five minutes to preserve their color and then placed in 70% alcohol.

2.29 Criteria for species and subspecies

Two similar forms are regarded as distinct species if their geographical ranges overlap and if they show no intergradation in at least one morphological character (color excluded). If a narrow stabilized hybrid belt is developed in the region of contact of two forms that are largely allopatric they are treated as distinct species (see Mayr 1963). Two allopatric forms that differ only in coloration are judged to be conspecific. Allopatric forms of a single species are regarded as being subspecifically distinct if 75 per cent of the individuals of one form are different from 97 per cent of the individuals of the other (see Mayr et al 1953). However, if a clinal series of intermediate populations is intercalated between two distinct populations that are widely allopatric subspecific names are not given.

There are two opposing views regarding the subspecies concept.

Wilson and Brown (1953) believe the subspecies concept to be subjective and arbitrary in the light of discordant variation, variation in microgeographic races, and the artificiality of quantitative methods of defining the formal lower limits of the subspecies as well as other reasons. Inger (1961), however, argues that Wilson and Brown tend to magnify exceptional cases, and that the subspecies concept despite its limitations has proved useful. It is this latter view that is followed in this text. Many more opinions regarding the subspecies concept are expressed in issues of *Systematic Zoology* (1953 - 1960).

3.0 MORPHOLOGY OF THE MALE GENITALIA OF THE NORTH AMERICAN SPECIES OF THE CICINDELA MARITIMA GROUP

3.1 Introduction

Several papers dealing wholly or in part with the male genitalia of American tiger beetles have been published (Horn 1930, Papp 1952, Rivalier 1954, and Rumpp 1957). Horn observes that for some races of Omus californicus Eschscholtz shape and size of the penis is characteristic. Papp presents a detailed study of the internal sac from which relationships of the Nearctic and Palearctic tiger beetles are deduced, while Rivalier classifies the entire Cicindela fauna of the Americas. Rumpp uses male genitalia in separating more clearly the species Cicindela praetextata LeConte and Cicindela californica Menetries. The present study deals with male genitalia of North American species of the Cicindela maritima complex.

Male genitalia of three or more specimens of each North American species of the maritima group were examined. The male armature consists of three relatively large sclerites: a median structure called the median lobe, penis, and aedoeagus (see Fig. 1); and a pair of lateral parameres, one on each side of the median lobe and articulating with its base. Inverted in the median lobe is the membranous internal sac that is everted from the dorso-apical portion of the median lobe during copulation.

Within each species the shape of the median lobe is quite

uniform. There is, however, a considerable amount of interspecific variation, particularly in form of the apex, that proves useful in distinguishing species of the maritima group from one another.

The internal sac comprises many folds, dark areas bearing microtrichia or aculeae, and sclerites. These fields of aculeae, and sclerites can be homologized within the species of the maritima group. Numbers are assigned to sclerites and letters are assigned to fields. This system of nomenclature follows that of Ball (MS) and is not synonymous with that of Papp.

When retracted in the abdomen the median lobe lies lengthwise, parallel to the longitudinal plane of the body of the beetle, and the opening of the internal sac is dorsal. When the median lobe is in a copulatory position the aperture of the internal sac is ventral. For each species drawings of the retracted median lobe and the inverted internal sac viewed from the dorsal and left sides are presented. In addition the shape of the apex of the median lobe is given separately for each species. Included also is a table of the various sclerites of the internal sac for each North American member of the maritima group.

3.2 Descriptions

Male genitalia of Cicindela duodecimguttata Dejean (Figs. 1 a, b, c, and 10).- The median lobe is of relative average breadth and length. Two broad, lateral flanges that occupy the apical region of the median lobe converge apically to form a marked tip which curves ventrally.

The inverted internal sac is clearly visible, in which three fields of aculeae are distinct. These darkened areas are labelled a, b, and c. Field a, which has a pebbly appearance is apical in the infolded position but it is basad when the internal sac is everted. Field b, ventral in position, is a finger-like projection of the membrane from which only the apical end is separate in the form of a tiny sac. When the internal sac is inverted b hangs inward with the free end nearest the apical end of the median lobe. Conversely this field projects outward the blind end of which remains oriented toward the apex of the median lobe when the internal sac is everted. Field c, is three quarters circular, anterior in the infolded position, and appears to serve as the apical limits of the everted internal sac.

Six sclerotized areas are present. Most noticeable is the flagellum (4) which is a slender strip, pointed apically, and widened and hooked at the base. A short rectangular sclerite (3) is present to the left of the base of the flagellum, and sclerite 5, a cuplike structure, lies posterior to 3. In Fig. 1 sclerite 5 lies to the right of the median line beneath several membranous folds, but it is more clearly shown in Fig. 2. To the left of and lying in part over the basal portion of the flagellum is sclerite 1, a quadrate plate. Sclerite 6 is oriented to the right of the sagittal plane. It is twisted basally and resembles an aculeate field apically. Sclerite 2 is an elongate curved strip with its apical end near that of the flagellum. A very small triangular sclerite is present between 2 and 6, but it is not numbered since it may be a disconnected piece of one of these two sclerites. This sclerite is illustrated with sclerite 2 in

Fig. 10.

Male genitalia of Cicindela oregona LeConte (Figs. 2, a, b, c, and Fig. 10).- Shape of the median lobe is quite different from that of the preceding species. Though the apical, lateral flanges are about as long as those of duodecimguttata they are rather narrow. The apex is not markedly curved ventrally. Fields and sclerites, excepting sclerite 5 which is relatively large, look like their counterparts of duodecimguttata.

Male genitalia of Cicindela depressula Casey (Figs. 3, a, b, c, and 10).- Unlike the penis of duodecimguttata, and oregona the apical portion of the median lobe in this species is characterized by wide lateral flanges that form a blunt tip. The flanges are continuous and not separated from one another by the raised apical section of the chamber containing the internal sac as they are in the two preceding species. The median lobe is short and broad.

Field a is composed of several elongate folds that together form a rough area. Field b is comparatively light, and c is c-shaped.

Sclerites 1, 2, 3, 4, and 6 are respectively of the shapes and in the positions described for those of duodecimguttata. At the basal end of sclerite 2 the small triangular sclerite is elongate. Sclerite 5, large and lightly sclerotized, is visible when the internal sac is everted or inverted.

Male genitalia of Cicindela repanda Dejean (Figs. 4, a, b, c,

and 10).- The portion of the median lobe that contains the internal sac is more apically confined than those of the three discussed species. The lateral flanges are narrow and widely separated dorsally by the chamber of the internal sac.

Field a is small and lightly aculeate, while b is a distinct area pebbly in appearance. Field c is of the common shape.

Sclerite 1 is large and triangular, while 2, 3, 4 and 6 are like those of duodecimguttata. The small sclerite near the basal end of 2 is absent. Sclerite 5, large and heavily sclerotized, is quite distinct.

Male genitalia of Cicindela limbata Say (Figs. 5, a, b, c, and 10).. The median lobe is relatively short and narrow. The two broad, lateral flanges are evenly rounded and together converge to a marked but non-protruding apex.

Fields a and b are strongly aculeate; and c is clearly indicated in the form of one third of a circle.

Variation is evident in the shape of sclerite 1 which is generally smaller in size than those of the other North American species of the maritima group.

Sclerites 2, 3, 4, and 6 are of the common shape, and sclerite 5 is absent.

Male genitalia of Cicindela bellissima Leng (Figs. 6, a, b, c, and 10).. The median lobe is of average length but thicker than those of the preceding species. From a dorsal view the lateral flanges compose a broad

apical region that terminates as a sharp projecting tip.

Field a is clearly indicated by its dark compact appearance. Both a and b have large and scale-like aculeae. Field c is three quarters of a circle.

Sclerites 1, 2, 3, 4, and 6 are each of the common shade intensity and shape. Sclerite 5 is absent.

Male genitalia of Cicindela columbica Hatch (Figs. 7, a, b, c, and 10).-- The median lobe is relatively long and slender, the apical region of which comprises two fairly wide lateral flanges that are slightly constricted basally, and an unprojected, rounded apex.

Prominent aculeae occur on field a, which is smaller and less compact than that of bellissima. Field b is a lightly shaded area, while c is of the common type.

Sclerites 1, 2, 3, 4, and 6 each resemble their counterparts in other species of the maritima group. The sclerite between 2 and 6 is large and heavily sclerotized. Sclerite 5 is small and field-like in appearance which makes it difficult to detect.

Male genitalia of Cicindela hirticollis Say (Figs. 8, a, b, c, and 10). --The median lobe is elongate and thick. The chamber which contains the internal sac is extended dorso-apically so that the lateral flanges are widely separated, and the apical portion of the median lobe is obscured when viewed from the dorsal side.

Field a is composed of several elongate folds; b is sparsely

aculeate; and c is a semicircle.

Sclerite 1 is relatively lightly sclerotized. Sclerites 2, 3, and 6 each have the shape characteristic of the maritima group. The sclerite between 2 and 6 is large and rectangular much like that of columbica. The apical twirl in sclerite 4 is markedly pronounced. Sclerite 5 is broad and lightly sclerotized.

Male genitalia of Cicindela theatina Rotger (Figs. 9, a, b, c, and 10).-- The median lobe is of average length and breadth the apical region of which somewhat resembles that of duodecimguttata without the protruding tip. A distinct keel is present on the ventral apical portion of the median lobe.

Fields a and b are strongly microtricheate and c is normal.

Sclerites 1, 2, 3, 4, and 6 are of the general shape and size. The sclerite between 2 and 6 is large. Sclerite 5 is barely visible and only occurs as a small roughened area.

3.3 Discussion

It is difficult to fix the genitalia of each species in the same relative position for drawing purposes. Thus sclerites that are of the same shape but drawn in different positions may appear to be different from one another. The shapes of sclerites 2, 3, 4 (excepting that of hirticollis), and 6 are remarkably constant throughout the North American maritima group. This uniformity in sclerite shape sets these species apart as a unit from other Cicindela groups. Some interspecific differences

of the internal sac are evident, however. These are: shape and size of sclerite 1; presence, absence, and size of the sclerite between 2 and 6; presence, absence, and condition of sclerite 5. The shape of the median lobe is diagnostic for each species, particularly the form of the apical region viewed from the dorsal or ventral sides.

Median lobes and internal sacs of specimens taken in the hybrid region of duodecimguttata and oregona were examined. It was found that the form of the apex of the median lobe changed from pure duodecimguttata to pure oregona through intermediate shapes.

4.0 TAXONOMY OF THE NORTH AMERICAN COMPONENTS OF THE CICINDELA MARITIMA GROUP

4.1 Diagnosis of the group

At the present time there is no generally accepted definition of the maritima group (repanda group, in part). Leng (1902) defined the repanda group on the basis of external characters in which repanda, hirticollis, oregona, and duodecimguttata, were brought together, but limbata and bellissima were excluded. Casey (1913) formed the repanda group on the basis of body size and shape of humeral lunule. The species limbata and bellissima were not included, and hirticollis was regarded as constituting a closely related but separate group. Papp (1952) used characters of the internal sac of the male genitalia for grouping members of the repanda complex (sensu Leng) together with other species, which, I believe, should have been included in other species groups. The diagnosis of the North American species of the maritima group made by Rivalier (1954, Group IV) is followed in this text. Rivalier united members of the repanda group with limbata and bellissima, but columbica and theatina were not mentioned.

The following combination of characters of the internal sac of the male genitalia are regarded as being diagnostic, and separate the North American species of the maritima group from other species groups of Cicindela (see Fig. 10): sclerite 1, a quadrate plate lying over the base of sclerite 4 (flagellum); sclerite 2, a flat, elongate, curved strip; sclerite 3, short, rectangular, and lying to the left of sclerite 4; sclerite 6, large twisted basally, and lightly sclerotized apically;

field a apical in the inverted position, roughened or densely aculeate;
 field b, a finger like projection, roughened or densely aculeate;
 field c, semi-circular shape, terminal in the everted position;
 chitinous tooth absent (defined by Papp, 1952).

4.2 Key to the North American species of the maritima group based on non-genitalic characters

- 1 Genae glabrous.....2
 Genae hairy¹6
- 2 (1) Posterior tip of humeral lunule (when present) usually with a
 slight anteriorly-directed hook; head with frons covered with
 numerous hairs.....C. hirticollis Say
 (not treated in detail).
 Posterior tip of humeral lunule not hooked; dorsum of head
 covered sparsely with hairs; OR glabrous; OR hairs clustered
 near the front inner edge of each eye.....3
- 3 (2) Marginal band of elytron absent.....4
 Marginal band of elytron present.....5
- 4 (3) Cluster of one to four hairs near each eye; shoulder of
 middle band (usually) smoothly rounded; vertex often with
 several very small hairs².....C. depressula Casey (sec. 4.43)

1. If hairs of the head or genae are abraded their former positions
 are indicated by tiny setigerous punctures.
2. Examine median lobe of male for a more positive identification
 (see Figs. 1 - 9).

Cluster of eight to 11 hairs near each eye; shoulder of middle band (usually) raised; vertex usually glabrous².....

.....C. oregona LeConte (Sec. 4.42)

- 5 (3) Frons sparsely hairy; humeral lunule elongate and markedly oblique; posterior tip of humeral lunule nearly touching shoulder of middle band.....C. bellissima Leng (not treated in detail).

Frons glabrous; humeral lunule short and slightly oblique; posterior tip of humeral lunule widely separated from shoulder of middle band.....C. columbica Hatch (not treated in detail).

- 6 (1) Humeral lunule c-shaped or in the form of two dots; elytral markings narrowly expanded or broken.....7

Humeral lunule oblique; elytral markings very broad, widely connected, or brown pigment of elytra greatly reduced obliterating basic elytral markings.....8

- 7 (6) Form broader than repanda; pronotum broad; marginal band absent or widely separated from humeral lunule³.....

.....C. duodecinguttata Dejean (Sec. 4.41)

Pronotum narrow; marginal band connected to humeral lunule³.....

.....C. repanda Dejean (not treated in detail).

3. Examine median lobe of male for a more positive identification.

- 8 (6) Elytra predominantly pale, elytral pattern completely obliterated.....C. limbata Say (not treated in detail).
Elytra predominantly dark.....9
- 9 (8) Marginal band broad and widely connected to other elytral markings, posterior portion of humeral lunule short.....C. theatina Rotger (not treated in detail).
Marginal band short connected only to middle band; posterior portion of humeral lunule very long.....C. limbata Say (not treated in detail).

4.3 Key to North American species of the maritima group based on the male genitalia

- 1 Median lobe with apical lateral flanges narrow.....2
Apical lateral flanges of median lobe broad.....4
- 2 (1) Chamber of internal sac extended dorso-apically; sclerite between 2 and 6 large; sclerite 4 with a pronounced twist.....C. hirticollis Say (Figs. 8, 10)
Chamber of internal sac not extended; sclerite between sclerites 2 and 6 small or absent; twist in sclerite 4 normal.....3
- 3 (2) Sclerite 5 large; sclerite between sclerites 2 and 6 absent; part of median lobe containing internal sac short.....C. repanda Dejean (Figs. 4, 10)

- Sclerite 5 normal size; sclerite between sclerites 2 and 6 small; part of median lobe containing internal sac elongate.....
.....C. oregona LeConte (Figs. 2, 10)
- 4 (1) Apical portion of median lobe with a distinct keel along median line.....C. theatina Rotger (Figs. 9, 10)
Keel absent.....5
- 5 (4) Apex of median lobe produced into a narrow tip.....6
Apex of median lobe blunt, not produced.....7
- 6 (5) Sclerite 5 absent; fields a and b densely aculeate.....
.....C. bellissima Leng (Figs. 6, 10)
Sclerite 5 normal size; fields a and b lightly aculeate.....
.....C. duodecimguttata Dejean (Figs. 1, 10)
- 7 (5) Lateral flanges of median lobe constricted basally; sclerite between sclerites 2 and 6 large.....
.....C. columbica Hatch (Figs. 7, 10)
Lateral flanges of median lobe not constricted; sclerite between sclerites 2 and 6 normal size.....8
- 8 (7) Sclerite 5 absent; fields a and b densely aculeate.....
.....C. limbata Say (Figs. 5, 10)
Sclerite 5 present; fields a and b lightly aculeate.....
.....C. depressula Casey (Figs. 3, 10)

4.4 The species Cicindela duodecimguttata Dejean, oregona LeConte and
depressula Casey

4.41 Cicindela duodecimguttata Dejean (Figs. 11, 13, 15)

Cicindela duodecimguttata Dejean 1825:73. Type locality--Amerique
septentrionale. Fall 1901:308. Leng 1902:148.

Blatchley 1910:34. Casey 1913:28. Horn 1915:374,
and 1930:80. Stainer 1934:247. Papp 1952:515.

Rivalier 1954:252. Lindroth 1955:16. Wallis 1961:
20. Graves 1963:498.

Cicindela bucolica Casey 1913:28. Type locality--Aweme,
Manitoba.

Cicindela hudsonica Casey 1916:29. Type locality--Hudson Bay
Territory.

Cicindela repanda edmontonensis Carr 1920:218. Type locality--
Edmonton, Alberta.

Cicindela duodecimguttata repanda, Horn 1930:81 (not Dejean);
Papp 1952:515.

This species is characterized by its dull brown dorsal surface,
and elytral maculations. Specimens of duodecimguttata are usually
distinguishable from specimens of the markedly similar species repanda.
In western areas, where these species are sympatric, individuals of
duodecimguttata have a broad prothorax, dark brown elytra, and widely
interrupted marginal bands, while specimens of repanda have a narrower
prothorax, lighter brown elytra, and the marginal bands are narrowly, or
not, interrupted. In eastern Canada the elytral pattern of duodecimguttata

generally is broken but repanda retains full elytral maculations excepting the subspecies novascotiae Vaurie that occurs on the Canadian Atlantic coast (see Vaurie 1951). Differences in male genitalia however, are clear and should be used for definitive identification (see Lindroth 1955:16-17, and section 3.2 of this thesis).

In western Canada, populations of duodecimguttata occur on the edges of lakes, ponds, rivers, streams, and sloughs wherever the soil is dark and wet and consists of mixtures of sand and clay, and clay or mud. This type of habitat is preferred by duodecimguttata on the mainland in eastern Canada, also (see Leng 1902, Blatchley 1910, and Graves 1963). Lindroth (1955) observed that in Newfoundland duodecimguttata specimens are found on sand and gravel, as well as on clay or humus.

Notes on synonymy

The name bucolica Casey has been given to specimens of duodecimguttata with full elytral markings. Such specimens are common in the western prairies. Casey's hudsonica, the elytral pattern of which is very reduced, is a variant of duodecimguttata. The name edmontonensis Carr was proposed for a variant of duodecimguttata that has a narrow elytral pattern. Horn (1930) treats repanda as a "larger" race of duodecimguttata and bucolica as a lesser form of repanda. Evidence for this synonymy is presented in the following section on geographic variation.

Geographic variation

This species inhabits a territory that extends from the eastern

front of the Rocky Mountains to the Atlantic seaboard, and from the Northwest Territories to Alabama (Fig. 17). Throughout the range of duodecimguttata, except for the zone of intergradation with oregona, two easily observed characters vary geographically: color of the dorsal surface of the body and elytral pattern. Variation in both features has been examined quantitatively. Variation in length of elytra has also been studied.

Size.- Average lengths of elytra, from the tip of the scutellum to the end of the elytral spine, were calculated for male and female specimens from 20 localities listed in Table 3. Character gradients are irregular and do not conform with latitudinal, longitudinal, or altitudinal changes. The mean lengths of elytra range from 6.57 mm to 7.60 mm for males, and 7.11 mm to 8.22 mm for females. Average elytral lengths of males and females from the island of Newfoundland (Harmon Field) are not larger than those of corresponding sexes from coastal localities of the adjacent mainland such as Bathurst, New Brunswick.

Coloration.- There are no color differences between sexes of duodecimguttata. Males and females are usually dull brown dorsally, metallic blue-green ventrally, and the thoracic pleura are coppery. The dorsal surface is the only area that is subject to color variation. In most regions the dorsum is dull brown, but in eastern Canada and United States, color varies.

Specimens from seven localities on or near the Atlantic seaboard were examined for color of the dorsal surface; the results

are listed in Table 1. Brown specimens are most abundant in all of the population samples, followed in number by brown-green or green and finally blue individuals.

The most variable maritime population sample is one collected at Yarmouth, Nova Scotia. The entire color range is represented. Brown specimens account for 55.8 per cent of the sample. Green, brown-green, and blue individuals follow in number in that order. Blue specimens are absent from the Goose Bay, Labrador, and Harmon Field, Newfoundland samples both of which are composed mainly of brown members, followed by brown-green and green. Only brown individuals occur in the Bathurst, New Brunswick population sample. Except for one green specimen from Keene Valley, New York, the inland samples are made up entirely of brown specimens. Green specimens are not uncommon in coastal populations of species of the maritima group (see o. oregona in subspecies section of this thesis; also r. novascotiae Vaurie 1951).

Color pattern of elytra.- The elytral pattern is fully developed in some duodecimguttata individuals and almost absent in others. The four main components of the elytral pattern vary independently. These were assigned numerical values to form a compound character index for analysing variation in elytral pattern. If all markings are complete a high score is assigned (Maximum value 11), and if the markings are greatly reduced a low value is assigned (minimum value 0). Markings that range between complete and reduced are given intermediate values. The components of the elytral pattern are illustrated in Fig. 15 and their assigned values are given in Table 2. As many eastern duodecimguttata specimens have maculations typical of oregona, the compound character index used

in this section was not employed in the hybridization section. A compound character index (hybrid index), based on the elytral pattern, was determined for each specimen of 20 population samples from different localities. Results are presented in Table 3. The average index value for each sample is indicated in Fig. 17. The samples are arrayed in five transects so that geographical variation in elytral maculations may be more clearly appreciated. Three transects-A-A', B-B', and C-C'- are on a west-east plane, while two -D-D', and C-C' - are oriented north to south.

An average index reduction from west to east is seen in the A-A' transect. The mean values 9.73 and 9.39 of the samples that represent Christopher Lake, Saskatchewan, and Le Pas, Manitoba, respectively, indicate full elytral markings. The mean index change per mile between these localities is about 0.00160. The mean index for the population sample from Ogoki, Ontario is 6.22 which is a change of 0.00488 index units per mile from that of The Pas, Manitoba. The trend is less marked between Ogoki, Ontario and Duparquet, Quebec the rate of change being 0.00320 index units per mile. A change in average index value of 0.00133 occurs between Duparquet, Quebec and Bathurst, New Brunswick; and a change of 0.00127 occurs between Bathurst, New Brunswick and Harmon Field, Newfoundland that have index values of 4.94, 4.11, and 4.54 respectively.

Average index values of the six population samples in transect B-B' compliment the trend shown in A-A'. Elytral maculations are quite full in the western localities as shown by average index values: Lethbridge, Alberta, 10.12; Bottineau County, North Dakota, 9.88; and Minnesota,

9.44. The rate of mean index changes per mile between Lethbridge, Alberta and Bottineau County, North Dakota is only 0.00041 and increases slightly to 0.00130 between Bottineau County, North Dakota and Minnesota. However, the average index value for the Cheboygan, Michigan specimens is markedly less than that of Minnesota sample, the rate of change being 0.00776 index units per mile. This is approximately six times the rate of change between Bottineau County, North Dakota and Minnesota. Mean index difference between eastern population samples are slight. Average values for areas follow: Cheboygan, 5.79; Keene Valley, New York, 5.21; and Yarmouth, Nova Scotia, 5.10. Their values express collectively an average reduction in the elytral pattern.

The southermost west-east transect, C-C', comprises the following population samples and their respective average index values: Bennett, Nebraska, 6.03; St. Louis, Missouri, 4.79; and Jeannette, Pennsylvania, 5.77. The mean index decreases 0.00355 units per mile between Bennett and St. Louis while between St. Louis and Jeannette there is a mean increase of 0.00158 units per mile.

Transect D-D' is oriented north to south near the western limits of the range of this species. The pattern of the elytra tends to increase north to south in the first part of the transect as follows: Christopher Lake, 9.71; Bottineau County, 9.88; and Wolsey, South Dakota, 10.00. The spatial mean change in index units between these population samples is negligible in contrast to that which occurs between Wolsey and Bennett (0.01498). The mean index value of Bennett is 6.03, and it is 5.10 for Texas. The three northern localities therefore have samples with full elytral markings, while specimens of

the two more southerly localities have reduced maculations with a sharp change occurring between Wolsey and Bennett.

A clinal north to south fragmentation in maculation of the elytra is evident in transect E-E'. Ogoki, Cheboygan, St. Louis, and Oktibbeha County, Mississippi each have population samples with mean index values of 6.22, 5.79, 4.79, and 3.40 respectively. The rate of increase in mean index units per mile is 0.00101 between Ogoki and Cheboygan, 0.00170 between Cheboygan and St. Louis, and 0.00376 between St. Louis and Oktibbeha County, Mississippi.

The population samples can be separated into two geographic groups by areas of marked rates of change in mean index values. The greatest difference in average index value is between The Pas, Manitoba and Ogoki, Ontario; between Minnesota and Cheboygan County, Michigan; and between Wolsey, South Dakota and Bennett, Nebraska. The species therefore may be divided into northwestern populations that have complete elytral markings, and southern and eastern groups that exhibit a more or less interrupted elytral pattern. However, the two aggregates of populations are not subspecifically distinct. A separation on the basis of the 75 per cent rule cannot be made because of extensive overlap in range of variation between the two groups of populations (see Table 3).

Breakdown of the elytral pattern has probably occurred independently in duodecimguttata, repanda, depressula and oregona and if so this is a good example of parallel evolution. Perhaps the breakdown of elytral pattern in duodecimguttata

is the result of a mutation that has spread throughout most populations except for those in the west.

Distribution

A total of 3,433 specimens was examined. One specimen is labelled Coal Creek, Colorado. This locality is far beyond the probable western limits of the range of duodecimguttata at that latitude, but the record cannot be completely ignored because Coal Creek is near the Arkansas River which runs eastward into duodecimguttata territory and may serve as a highway for pioneering populations of this species.

Canada. ALBERTA: Andrew, 3; Beaver Hill Lake, 1; Bilby, 14; Chin, 8; Cooking Lake, 7; Cypress Hills, 2; Doussal, 1; Drayton Valley, 4; Edmonton, 95; Falles, 1; Flatbush, 1; Fort Chipewyan, 1; Halfway House, 3; Jct. Rte. 39 and North Saskatchewan River, 11; Lake Cardinal, 2; Lesser Slave Lake (east end), 1; Lethbridge (St. Mary's River), 5; Lethbridge (Six-mile Coulee), 310; Louis Bull Reservation, 3; McMurray, 18; Medicine Hat, 5; mile 7 on Smith-Fitzgerald Road, 1; Redwater, 2; Stirling Lake, 1; Tilley, 1; Tofield, 19; Vilna, 1; Wabamun, 3.

LABRADOR: Goose Bay, 29. MANITOBA: Aweme, 12; Baldur, 1; Beaver Lake, Riding Mountain, 2; Berens River, 9; Birtle, 1; Brandon (15 miles south), 2; Carberry (5miles west), 1; Clear Lake, Riding Mountain, 2; Dauphin, 5; Delta, 3; Douglas, 1; Gladstone, 2; Glenboro, 1; Grunthal, 1; Hilton (6 miles south), 21; Holland, 2; Husavick, 3; Kelwood, 1; The Pas, 23; Magnuls, 1; Makinock, 5; Marchand, 1; Max Lake, Turtle Mountain, 10; Melita, 1; mile 360, Rte. 10, 1; Morris, 1; Ninette, 25; Norgate (5 miles west), 5; Oak Lake (4 miles west), 1; Red River, 1; Red Rock Lake, 1;

Rennie (15 miles east), 1; Riding Mountain, 7; Rounthwaite, 1; Sandilands, 3; Shilo (5 miles south west), 4; Shoal Lake, 1; Silver Falls, 2; South Junction, 3; Stonewall, 1; Treesbank, Assiniboine River, 35; Vassar, 1; Victoria Beach, Lake Winnipeg, 8; Wanless, 1; Wasagaming, 1; Watson's Lake, 1; Waugh, 1; Westbourne, 5; Whitemouth, 1. NEW BRUNSWICK: Apohaqui, 1; Bathurst, 19; Chipman, 6; Penobsquis, 3; St. John, 1; Sackville, 3; Shediac, 10. NEWFOUNDLAND: Bay of Islands, 4; Bay St. George, 13; Codroy, 11; Deer Lake, Humber River, 2; Gander, 14; Harmon Field, 59. NORTHWEST TERRITORIES: Fort Smith, 163; Hay River (Great Slave Lake Shore), 1; Seven Mile Lake (26 miles west Fort Smith), 6; Resolution, 5. NOVA SCOTIA: Armdale, 3; Baddeck, 2; Barrington Passage, 1; Boisdale, 16; Cape Breton, 35; Cow Bay, 29; Bigby, 1; Great Village, 8; Halifax, 1; Ingramport, 5; Kedgemakooze Lake, 2; Kentville, 11; Lockeport, 2; North Sidney, 9; Port Maitland, 36; Queens, 2; Turuo, 10; Weymouth, 1; Wilmot, 1; Yarmouth, 52. ONTARIO: Agawa Bay, Lake Superior, 1; Coniston, 3; DeCew Falls, 1; Goderich, 1; Gravenhurst, 1; Hamilton, 2; Hearst (65 miles west), 23; Hudson Bay, 1; Ingolf, 9; James Bay, 1; Kearney, 6; Kenora (14 miles east), 1; Lake of the Woods, Harris Hill, 2; Loleo, 7; Minnitaki, 1; Moose Factory, 6; Ogoki, 46; Ojibway, 1; One Sided Lake, 2; Ottawa, 2; Port Arthur, 3; Powasson, 2; Sibley Provincial Park, Middlebrun Bay, Lake Superior, 7; Sudbury, 1; Toronto, 5; Ventnor, 2; Woodtick Island, 1. QUEBEC: Baie Comeau, 1; Cap Rouge, 1; Cascapedia, 2; Charlevoix County, 4; Duchesnay, 6; Duparquet, 17; Gaspé, 5; Joliette, 2; Knowlton, 2; Lachute, 2; Ladysmith, 1; Lake Blanch, 12; Lac Opasatika, 1; Mont Joli, 2; Mont Lyall, 2; Montreal, 2; Natashquan, 1; Otter Lake, 12;

St. Alexandre, 1; Ste. Anne de Monts, 1; Val Morin, 1. SASKATCHEWAN: Big River, 16; Broadview, 4; Candle Lake, 3; Ceylon, 1; Christopher Lake, 24; Cut Knife, 4; Estevan, 2; Fish Lake, 1; Glaslyn, 3; Good Spirit, 10; Holbein, 1; Kenosee, 11; Lake Manitou, 1; Neat Frys, 9; Pike Lake, 1; Pike Lake Park, 41; Regina, 1; Saskatoon, 22; Val Marie, 2; Waskisiu Lake, 10; White Fox, 12; Yorkton, 2.

United States. ALABAMA: Chilton County: Coosa River, 1. Tuscaloosa County, 1. ARKANSAS: Boone County: Harrison, 2. Lawrence County, 1. Washington County: Fagett, 1. Localities of unknown counties: Ozark Mountains, 11. COLORADO: Fremont County: Coal Creek, 1. CONNECTICUT: Litchfield County: Cornwall, 3; Litchfield, 2; Torrington, 3; Twin Lakes, 4; Washington, 2. New Haven County: Meriden, 7. DELEWARE: New Castle County: Newark, 6. GEORGIA: Fulton County: Atlanta, 8; East Point, 1. Habersham County: Cornelia, 1. Localities of unknown counties: Georgia, 1. ILLINOIS: Champaign County: Champaign, 1; Urbana, 4. Cook County: Chicago, 17; Cook County, 2; Flossmoor, 3; Palos Park, 2; Summit, 10. Fayette County: Ramsey, 2. Lake County: Antioch, 1; Cedar Lake, 3; Lake County, 1; Waukegan, 3. McHenry County: Algonquin, 3; McHenry, 1; Richmond, 3. McLean County: Bloomington, 1; Normal, 2. Macon County: 1. Marshall County: Taluca, 1. Ogle County: White Pines Forest, 6. Peoria County: Peoria, 4. Perry County: Pyem, 1. Piatt County, Atwood, 1. Putnam County: 2. Randolph County: Chester, 3. Rock Island County: Moline, 1. Union County: Ware, 3. Will County: New Lenox, 1. Williamson County: Crab Orchard Lake, 1. Localities of unknown counties: Dune Park, 1. Edgebrook, 16. Funks Grove, 4. Illinois, 1. Rock, 1. INDIANA: Cass County: 1. Gibson County: 2.

Jefferson County: Hanover, 1. Knox County: Vincennes, 1. Porter County:
 Beverley Shores, 1. Posey County: 3. Starke County: North Judson, 12.
 Tippecanoe County: Lafayette, 3. Localities of unknown counties: Lake
 Station, 1. Mineral Springs, 3. Pine, 1. T. R. P. Indiana, 1. IOWA:
 Boone County: Boone, 27. Cerro Gordo County: Clear Lake, 1. Clayton
 County: Guttenberg, 1. Dickinson County: Lake Okoboji, 3. Henry
 County: Mount Pleasant, 1. Howard County: Elma, 1. Johnson County:
 Iowa City, 4. Lee County: Fort Madison, 1. Story County: Ames, 2.
 Woodbury County: Sioux City, 1. Localities of unknown counties: Iowa, 1.
 Silver Lake, 1. KANSAS: Atchison County: Atchison, 3. Bourbon County:
 Fort Scott, 3. Coffey County: Burlington, 1. Douglas County: 3. Ellis
 County: 1; Hays, 1. Johnson County: Argentine, 14. Leavenworth County:
 Leavenworth, 7. Pottawatomie County: Onaga, 8. Riley County: 1. Saline
 County: Salina, 1. Shawnee County: Topeka, 11. Trego County: Wakeenay, 1.
 Localities of unknown counties: Central Kansas, 1. KENTUCKY: Localities of
 unknown counties: Kentucky, 3; Kentucky near Cincinnati, Ohio, 1. MAINE:
 Hancock County: Bar Harbor, 1; Mount Desert, 6; Seal Harbor, 7.
 Kennebec County: Monmouth, 12. Piscataquis County: Greenville, 1; Mount
 Katahdin, 1. York County: Agamenticus, 2. Localities of unknown counties:
 Bass Harbor, 2; Maine, 1; Pleasant Ridge, 5; Wales, 2. MARYLAND:
 Allegany County: Mount Savage, 4. MASSACHUSETTS: Berkshire County:
 Benedict Pond, 2; Lenox, 4. Bristol County: Rehoboth, 2. Middlesex
 County: Framingham, 19; Sherborn, 9. Norfolk County: Sharon, 1.
 Plymouth County: 3. Suffolk County: Cambridge, 1; Medford, 1;
 Stoneham, 1. Worcester County: Southboro, 2. MICHIGAN: Alger County:
 2; Onota Twp., 10. Allegan County: Allegan State Forest, 1; Rabbit
 River, 1. Alpena County: Alpena, 1; Squaw Bay, 2. Arenac County: White

Stone Point, 1. Berrien County: Sawyer Dunes, 1. Cass County: 1.
 Charlevoix County: Beaver Island, 1; Thumb Lake, 1. Cheboygan County:
 16; Douglas Lake, 84. Chippewa County: Marquette N. F., 1; Neebish
 Island, 4. Clare County: 8-Point Lake, 1. Delta County: Garden, 1.
 Genesee County: Davison T. W. P., 1; Flint, 1. Gogebic County: 12;
 Black River Park, 4. Huron County: Pte. Aux Barques, 2; Port Austin,
 1; Sand Point, 1. Ingham County: 1. Ionia County, 1. Iosco County:
 2; State Game Refuge, 1. Keweenaw County: Copper Harbor, 1; Eagle
 Harbor, Lake Superior, 10; Manganese Lake, 11. Lapeer County: Hadley
 T. W. P., 1. Mackinac County: 1; St. Ignace, 3. Marquette County:
 Huron Mountains, 12; Marquette, 1. Menominee County: Daggett, 1.
 Monroe County: Erie, 1. Montmorency County: 3. Ontonagan County:
 Gogebic Lake, 15. Otsego County: 2; Vanderbilt, 1. Schoolcraft County:
 Germfask, 1. Tuscola County: Bay Park, 2. Wayne County: Detroit, 6.
 Washtenaw County: Ann Arbor, 12. Localities of unknown counties: Pcn.
 Ind., 1; Michigan, 2. MINNESOTA: Aitkin County: Aitkin, 1. Anoka
 County: 2. Becker County: 5. Beltrami County: Waskish, 3. Carlton
 County: Moose Lake, 3. Carver County: Lake Waconia, 2. Clearwater
 County: 14; Gonvick, 1. Hennepin County: 1; Minneapolis, 2.
 Koochiching County: Rainy Lake, 3. Lac Qui Parle County: 3. Lake
 County: South Kawishiwi, 1. Lake of the Woods County: Williams, 1.
 Le Sueur County: 1. Nicollet County: St. Peter, 5. Renville County:
 Bird Island, 1. Roseau County: Roseau, 2. St. Louis County: Duluth, 2.
 Scott County: Jordan, 1. Stearns County: Koronis Lake, 6; Rice Lake, 10.
 Traverse County: 3. Wilkin County: Rothsay, 1. MISSISSIPPI: Oktibbeha
 County: 12; A & M College, 72. Tippah County: Tiplersville, 2. MISSOURI:
 Caldwell County: Hamilton, 13. Carter County: Van Buren, Ozarks Mountains, 2.

Greene County: Springfield, 2; Willard, 8. Linn County: 1. Pike County: Louisiana, 7. St. Louis County: St. Louis, 19; Valley Park, 2.

MONTANA: Cascade County: Ulm, 1. Chouteau County: Fort Benton, 1. Hill County: Fresno, 2. Roosevelt County: Brocton, 1. Teton County: Chouteau, 3. Toole County: Dunkirk (8 miles south), 5. NEBRASKA: Dawes County: Wayside, 5. Lancaster County: Bennet, 73; Lincoln, 25; Malcolm, 31. Sarpy County: Bellevue, 1. NEW HAMPSHIRE: Carroll County: Ellis River Road, Jackson, 1; Wildcat Bank, Jackson, 1. Cheshire County: Jaffrey, 2. Coos County: Gorham, Peabody River, 4; Jefferson, 25; Israel River, Jefferson, 10. Grafton County: Twin Mountain, 21. Hillsboro County: Antrim, 1. Sullivan County: Meriden, 12. Localities of unknown counties: Glen House, White Mountains, 2; Martin Loe'n, White Mountains, 3; New Hampshire, 4; White Mountains, 1. NEW JERSEY: Bergen County: Ramsey, 1. Cape May County: Ocean City, 3. Essex County: South Orange, 1. Hudson County: Arlington, 6; Snake Hill, 5. Middlesex County: Jamesburg, 10; Milltown, 2. Passaic County: Paterson, 1. Salem County: Canton, 2. Sussex County: Lake Hopatcong, 1. Localities of unknown counties: Frieses Mill, 1; Manchester, 1; New Jersey, 2. NEW YORK: Cortland County: McLean Bogs, 1. Delaware County: Stamford, 3. Erie County: Buffalo, 1; Ebenezer, 1. Essex County: Ausable Lakes, 1; Elizabeth Town, 1; Heart Lake, 5; Jay Mountains, 1; Keene Valley, 46; Lake Golden, 1; Mount Whiteface, 3; Wilmington, 4. Franklyn County: Duane, 1. Fulton County: 1. Genesee County: Bergen, 6. Hamilton County: Lake Pleasant, 4; Racquet Lake, 3. Nassau County: Freeport, 1. New York County: New York City, 5. Niagara County: Lockport, 3. Onondaga County: White Lake, 5. Orangel County: Pine Island, 3. Oswego County: Minetto, 2. Queen's County: Far Rockaway, 1. Richmond County: Clover Valley, Staten Island, 1;

Hugenot, Staten Island, 1. St. Lawrence County: Cranberry Lake, 2.

Tompkins County: Ithaca, 16. Warren County: Lake George, 1; Stamford, 3. Localities of unknown counties: Big Island, 3; Clearwater, 1; Luzerne, 1; Quaker Hill, 2. NORTH CAROLINA: Buncombe County: Black Mountains, 1. Guilford County: Jamestown, 1. Mecklenburg County: Charlotte, 2. Moore County: Manly, 2; Southern Pines, 2. Orange County: Chapel Hill, 2. Localities of unknown counties: Morrison, 6.

NORTH DAKOTA: Benson County: 2. Bottineau County: 73; Lake Metigoshe, Turtle Mountain, 8; Omemee, 3. Burleigh County: 3; Bismark, 1. Burke County: 4. Cass County: Fargo, 1. Cavalier County: 4. Divide County: 4. Eddy County: New Rockford, 14; Sheyenne River, 3. Kidder County: Tappen, 1. Logan County: 4. McHenry County: 14. McLean County: 1. Morton County: 3. Nelson County: 4; Stump Lake, 3. Pembina County: 1. Ransom County: 3. Rawsey County: 1. Renville County: 8. Richland County: 2. Rolette County: 10; Golden Lake, Turtle Mountain, 2. Sheridan County: 2. Ward County: 4. Wells County: 1. Williams County: 3. Localities of unknown counties: Jarves Lake, 1; Mooreton, 3.

OHIO: Ashtabula County: Ashtabula, 2; Jefferson, 17. Delaware County: 1. Franklin County: Columbus, 10. Gallia County: Vinton, 3. Hamilton County: Cincinnati, 4. Hocking County: 1. Licking County: Bowling Green Trail, 4; Newark, 1. Localities of unknown counties: Crane Hollow, 1.

OKLAHOMA: Blaine County: Roman Nose State Park, 3. Cleveland County: Norman, 2. Garfield County: Enid, 1. Johnston County: 1. Kay County: Newkirk, 2. Kingfisher County: Kingfisher, 1. Murray County: Sulphur, 5. Noble County: Perry, 7. Payne County: Lake Carl Blackwell, 1; Stillwater, 1. Localities of unknown counties: Blue Jacket, 3; Centralia, 1; Wyandotte, 1. PENNSYLVANIA: Allegheny County: 5; Fair Oaks, 2; Westview, 1. Crawford

County: Meadville, 1. Cumberland County: Mount Holly, 1. Delaware
 County: 4; Lansdowne, 4. Forest County: Endeavor, 1. Mercer County:
 Sharpsville, 1. Montgomery County: 1. Philadelphia County: Lawndale,
 1; Philadelphia, 3. Warren County: Bear Lake, 1. Westmoreland County:
 Jeannette, 31. Localities of unknown counties: Castle Rock, 7;
 Pennsylvania, 1; Springfield, 2; Wall, 1. RHODE ISLAND: Providence
 County: Elmwood, 5. Washington County: Misquamicut, 2. SOUTH
 CAROLINA: Greenville County: Greenville, 1. Pickens County: Clemson
 College, 5. Richland County: Columbia, 11. SOUTH DAKOTA: Beadle County:
 Wolsey, 17. Fall River County: Hot Springs (5 miles south), 1. Lawrence
 County: Deadwood, 1; Savoy, 2. Meade County: Sturgis, 3. Moody County:
 Colman, 2. Pennington County: Rapid City, 1. Localities of unknown
 counties: South Dakota, 1. TENNESSEE: Knox County: Knoxville, 2.
 Pickett County: 1. TEXAS: Blanco County: 1. Dallas County: 1;
 Dallas, 10. Randall County: Canyon, 1. Washington County: Burton, 2.
 Localities of unknown counties: Cyp. Mills, 1; Texas, 4. VERMONT:
 Bennington County: Mount Equinox, 2. Localities of unknown counties:
 Vermont, 1. VIRGINIA: Bath County: Warm Springs, 4. Lee County:
 Pennington Gap, 1. Nansemond County: Suffolk, 2. Localities of
 unknown counties: Black Pond, 1; Virginia, 1. WEST VIRGINIA: Wyoming
 County: Pineville, 3. WISCONSIN: Bayfield County: Lake Namekagon, 1.
 Clark County: Wordon Township, 1. Dane County: 2. Dodge County: Beaver
 Dam, 10. Douglas County: Superior, 1. Kewaunee County: Kewaunee, 1.
 Milwaukee County: Milwaukee, 1. Vilas County: Tenderfoot Lake, 1.
 Walworth County: Allens Grove, 2. Waukesha County: Oconomowoc, 1.
 Waupaca County: Waupaca, 1. Wood County: Cranmoor, 4. Localities of
 unknown counties: Walker, 1; Wisconsin, 1. WYOMING: Crook County: Alva
 (6 miles east), 3; Devil's Tower, 6. Sheridan County: Sheridan (8 miles

TABLE 1. - Data on variation in color of dorsal surface of specimens from
seven eastern localities.

Locality	Brown		Brown/Green		Green		Blue		Total
	No.	%	No.	%	No.	%	No.	%	N
Goose Bay, Labr.	16	55.2	12	41.4	1	3.4	-	-	29
Harmon Field, Nfld.	41	69.5	14	23.8	4	6.7	-	-	59
Bathurst, N.B.	19	100.0	-	-	-	-	-	-	19
Yarmouth, N.S.	29	55.8	8	15.4	11	21.1	4	7.7	52
Duparquet, Que.	17	100.0	-	-	-	-	-	-	17
Keene Valley, N.Y.	45	98.0	-	-	1	2.0	-	-	46
Jeannette, Pa.	31	100.0	-	-	-	-	-	-	31

TABLE 2. - Values assigned to elytral markings of duodecimguttata specimens
for determination of compound character indices.

Elytral markings	Values			
	3	2	1	0
Humeral lunule	full	broken	2 dots	1 dot
Middle band	full	broken	2 dots	1 dot
Apical lunule	full	broken	2 dots	1 dot
Marginal band	-	full	trace	absent

TABLE 3. - Data on variation in compound character index values of specimens
of duodecimguttata from 20 localities.

Localities	Compound character index values											N
	1	2	3	4	5	6	7	8	9	10	11	
Fort Smith, N.W.T.			4	2	8	7	10	12	32	70	17	162
Lethbridge, Alta.					2	3	3	6	27	162	107	310
Christopher L. etc. Sask.			1			1	2	2	6	33	12	57
The Pas, Man.					1	2	1		3	11	5	23
Bottineau Co., N.D.					2		1	5	6	40	20	74
Minnesota					1	4	6	4	12	28	18	73
Wolsey, Beadle Co., S.Dak.							1		1	11	4	17
Bennet, Lancaster Co., Nebr.			9	9	13	8	18	12	2	3		74
St. Louis, St. Louis Co., Mo.			3	8	4	1	2			1		19
Texas			3	6	5	2	1	2	1			20
Ogoki, Ont.		1	4	7	7	9	5	4	2	7		46
Cheboygan Co., Mich.			10	15	25	21	9	10	5	5		100
Oktibbeha Co., Miss.		1	61	12	2	4		1				81
Duparquet, Que.	1		4	3		8		2				18
Keene V., Essex Co., N.Y.			8	12	9	5	3	1	3	1	1	43
Jeannette, Westmoreland Co., Pa.			4	7	6	4	4	1	2	2	1	31
Goose Bay, Labr.		1		6	11	2	3	2	1	3		29
Bathurst, N.B.			8	6	3		1	1				19
Yarmouth, N.S.		1	4	15	15	10	3	2	1	1		52
Harmon Field, Nfld.		2	15	20	9	6	2	3	1		1	59

4.42 Cicindela oregona LeConte (Figs. 12, 14, 16)

Cicindela oregona oregona LeConte 1857:41. Type locality--Oregon Territory and northern California as far as San Francisco. Fall 1901:308. Leng 1902:149. Casey 1913:29. Horn 1915:377, and 1930:82. Varas Arangua 1928:247. Tanner 1929:83. Papp 1952:514. Hatch 1953:41 (see Hatch 1953 for more references to C. o. oregona). Cazier 1954:242. Rivalier 1954:252. Wallis 1961:22.

Cicindela guttifera, Fall 1901:308.

Cicindela guttifera, Leng 1902:150.

Cicindela depressula scapularis Casey 1909:272. Type locality--California.

Cicindela guttifera sonoma Casey 1913:29. Type locality--California (maritime regions north of San Francisco). Horn 1915:378.

Cicindela quadripennis Casey 1913:30. Type locality--Hawthorne, Nevada. Horn 1915:378.

Cicindela ovalipennis Casey 1913:30. Type locality--Hawthorne, Nevada. Horn 1915:378.

Cicindela oregona scapularis, Horn 1915:378.

Cicindela oregona guttifera LeConte 1857:42. Type locality--New Mexico. Leng 1902:41. Horn 1915:378, and 1930:82. Varas Arangua 1928:250. Tanner 1929:83. Cazier 1954:242. Wallis 1961:22.

Cicindela sterope Casey 1913:28. Type locality--Kansas. Horn 1915:378.

Cicindela audax Casey 1913:29. Type locality--Colorado. Horn 1915:378.

Cicindela guttifera, Casey 1913:29.

Cicindela oregona oregonella Casey 1924:16. Type locality--
Parowan, Utah.

Cicindela duodecimguttata, Hatch 1953:38 (not Dejean).

Cicindela oregona guttifera x Cicindela oregona maricopa

Cicindela provensis Casey 1924:15. Type locality--Parowan and
Provo Canyon, Utah.

Cicindela provensis mormonella Casey 1924:15. Type locality--
Eureka, Provo Canyon, Parowan and Vineyard, Utah.

Cicindela provensis nephiana Casey 1924:16. Type locality--
Parowan, Utah.

Cicindela oregona maricopa, Tanner 1929:83 (not Leng).

Cicindela oregona maricopa Leng 1902:150. Type locality--Phoenix,
Arizona. Horn 1915:378. Horn 1930:82.

Cicindela guttifera maricopa, Casey 1913:27. Varas Arangua
1928:250.

Cicindela oregona navajoensis Van Dyke 1947:155. Type locality--
Kayenta, Arizona.

On the basis of a patch of hairs confined to the front inner edge of each eye (Fig. 12) this species may be distinguished from all other tiger beetles of the maritima group, except depressula, and female scutellaris Say. Female scutellaris and oregona specimens usually can be distinguished from each other simply by noting the geographical location from which the specimens were taken. The range of scutellaris is situated east of the Rocky Mountains while oregona occurs in the west limited by the eastern foothills of the Rockies. Specimens of the subspecies scutellaris scutellaris are present in

Colorado and New Mexico (Shelford 1917) but these forms are quite different from oregona in that they have bright cupreous to red elytra. Another subspecies of scutellaris, related to the subspecies criddlei, also occurs in Colorado (Rumpp 1961) and it is characterized by broad white margins of the elytra. The species depressula and oregona, on the other hand are sympatric. Individuals of these two species can be told apart by the numbers of hairs forming the clusters near each eye. The species oregona normally has eight to eleven hairs in this area while depressula usually has one to three and rarely four (see Sec. 4.43). A more reliable character for distinguishing between oregona and depressula is the shape of the median lobe of the male (see Sec. 3.2).

Like most other species of the maritima group oregona lives along the edges of rivers, lakes, sloughs etc. and it is found on a variety of substrates. I have taken oregona on sandy beaches, gravelly banks, and indeed on bare rock. This species is more common where there are open patches of beach.

Notes on synonymy

Casey proposed the names C. quadripennis and C. ovalipennis for male and female C. o. oregona specimens, respectively, that occur in Hawthorne, Nevada. Similarly C. oregona specimens collected north of San Francisco, were regarded by Casey as a subspecies of guttifera and he applied the name sonoma to them. Casey also considered a coastal blue form of o. oregona to be a subspecies of depressula and named it scapularis. However scapularis does not itself occur in uniform geographic populations and consequently I have not given it taxonomic status (see Wallis 1961).

Casey's audax and sterope are both forms of o. guttifera. Their original descriptions indicate these names refer to typical guttifera specimens that exist in Colorado and New Mexico. The name o. oregonella Casey has been given to specimens from highly variable populations of o. guttifera which occur in north central Utah. C. provensis Casey refers to blue specimens that were taken in Parowan and Provo Canyon, Utah. Parowan is located in southwestern Utah, a hybrid area of o. guttifera and o. maricopa, and Provo Canyon is situated in north central Utah where o. oregona and o. guttifera intergrade. The name provensis represents hybrid individuals of these regions.

Tanner regarded guttifera x maricopa and guttifera x oregona hybrid specimens in Utah as being variants of o. maricopa.

Geographic variation and subspecies

The species Cicindela oregona ranges widely in the west, from Alaska to southwestern California, Arizona and New Mexico and eastward to the Rocky Mountains (Fig. 18). Five easily observed characters vary geographically: body size, color of thoracic pleura, color of elytra, color of pronotum, and expanse of elytral pattern. Variation in these features is illustrated by measurement tables, pie-graph maps and pictorialized scatter diagrams. Length of elytra is expressed in millimeters from the tip of the scutellum posteriorly to the tip of the elytral spine along the suture. Width of elytra is similarly expressed in millimeters from the median line of the elytra through the transverse portion of the middle band to the elytral margin. This represents the

width of one elytron. These data are listed separately in Tables 4 and 5 for males and in Tables 7 and 8 for females. Tables 6 and 9 summarize data on variation in diameters of apical dots of males and females respectively. The measurements illustrate variation in expanse of the elytral pattern. The apical dot was measured transversely across the widest portion.

Size.- Before discussing the geographical aspects of size variation, I would note that females on the average are larger than males of the same population in every locality listed in Tables 4, 5, 7, and 8. This is true for the sexes in the same locality, but is not necessarily true if opposite sexes of different regions are compared. For example, females from Trinidad, Colorado have a mean elytral length of 7.23 mm while the average elytral length of males that are from Tanana River, Alaska is 7.26 mm. Data on variation of elytral length in males and females are given in Tables 4 and 7 respectively.

Three geographical routes (A, B and C in column 1 of Tables 4 to 9) have been selected to facilitate description of geographical variation in the length and width of elytra and expanse of color pattern. Tanana River, Alaska and Terrace and Oliver, British Columbia serve as the northern portion for all three routes. The first transect of population samples (A) extends from Alaska, south to New Mexico through British Columbia, Montana, Wyoming and Colorado. A second line of samples (B) is from Alaska to Arizona by way of British Columbia, Idaho and Utah. A third course (C) is from Tanana River, Alaska to southern Nevada, through British Columbia and Idaho. The data in Tables 4 to 9 are arranged to correspond to these routes. In the tables, latitudes and altitudes are listed in columns

3 and 4 respectively.

Because the corresponding character gradients of males and females are generally parallel, only the male samples are discussed in detail, with occasional reference to female samples. Table 4 indicates a decrease in the mean length of elytra of males, from north to south for all three courses. Each cline is quite irregular and there are sharp decreases and increases throughout. These rapid deviations in the character gradients appear to be correlated, at least in part, with a marked change in altitude or with a geographic barrier. However, I have noted discrepancies in the clines that cannot be related to the above factors.

Through the northern section of the first route there is a southward decrease in average length of elytra of 0.007 mm per degree of latitude for males and 0.018 mm per degree of latitude for females. From Alaska to Lower Medicine Lake, Montana a distance of $14^{\circ} 30'$ of latitude, no marked deviations occur in the trend. Between Lower Medicine Lake and Hardy, Montana however, a distance of only $1^{\circ} 19'$ latitude, mean length decreased by 0.20 mm. There is a drop of 1,500 feet in altitude between these two localities. Another irregularity in the above character gradient occurs between Helena and Gardiner, Montana - an increase in mean Length of elytra of 0.18 mm with $1^{\circ} 30'$ of latitude. Gardiner is 1,640 feet higher than Helena and contrast in elevation again seems to be related to the clinal difference. Population samples from Gardiner, Montana, Yellowstone National Park, Jackson Hole National Monument, and Moran, Wyoming have elytra of approximately equal length. Immediately southward the slope of the character gradient decreases markedly between Moran and Labarge, Wyoming.

Both sites are at approximately the same altitude and there are no visible geographic barriers between the two localities. In the Labarge and Green River regions the reduction in body size may be due to local factors such as disease, lack of food or marginal habitats (see Mayr 1963). Jelm and Saratoga in western Wyoming are rather isolated from Fort Bridger and Green River, in eastern Wyoming by the Great Divide Basin and the Continental Divide which are situated in south central Wyoming. East to west gene flow between populations of Cicindela oregona is most likely impeded in southern Wyoming by the presence of these geographical factors and their effect may at least partly, account for the presence of shorter elytra in eastern Wyoming. The difference between the average elytral lengths of males from Jelm and Fort Bridger is statistically significant but that between females is not.

The second arbitrary line of population samples (B) is from Alaska to Arizona by way of British Columbia, Idaho, and Utah. A clinal decrease in length of elytra is evident throughout this route as well. In Utah, the Alta, Mount Timpanogos and Provo Canyon populations have relatively very long elytra. The elevation of Alta is 8,585 feet; Mount Timpanogos is 11,750 feet; and Provo Canyon is located in Provo Park which rises to a height of 11,068 feet. Samples collected at lower elevations in areas adjacent to the above mentioned, have a shorter mean elytral length and populations from Stockton and Provo are examples of these. Population samples taken in Salt Lake City may have been collected in any of the creeks entering the city from the Wasatch range which serves as the eastern geographic limits of the metropolis. Although the insects were labeled as being collected in Salt Lake City, they could conceivably

have been taken at a much higher altitude nearby. Floy, Utah and Kayenta, Arizona have populations with the shortest elytra in the entire span of this gradient. South of Kayenta the samples taken in Prescott, Phoenix and Globe, Arizona are larger and compare in size with those from Idaho. These large forms in central and southern Arizona are fairly isolated and common only in these areas (see oregona maricopa in subspecies section).

The third line of population samples (C) extends from Alaska, south through British Columbia and Idaho to Nevada. Even though elytra are generally shorter in more southerly latitudes, the Walker Lake, Nevada population sample has the value for mean length of elytra equal to that of Tanana River, Alaska. I cannot account for this discrepancy.

Data on the variation in width of elytra are presented for males in Table 5 and for females in Table 8. There is a slight decrease in width of the elytra from Alaska, southward along all three routes. Irregularities in the clines of elytral widths correspond with changes in the character gradients of the lengths of elytra. At higher elevations of Montana, Wyoming and Utah mean values for elytral width are generally slightly greater than those of Alaska and Terrace, British Columbia. Tiger beetles of this species living in these lower latitudes at high altitudes are normally shorter but wider than their counterparts in boreal areas. This is especially marked in females. For example compare population samples of Tanana River, Alaska, Terrace and Queen Charlotte Islands, British Columbia with Gardiner, Montana, Alta and Provo Canyon, Utah, and Yellowstone National Park, Wyoming in Table 7 and 8.

Populations in Nevada are generally larger in average dimensions

of length and width than samples from Utah, Colorado and Wyoming at similar elevations; but east-west clines are very irregular.

Specimens collected in Queen Charlotte Islands, British Columbia are the only insular members recorded in Tables 4 to 9. The Queen Charlotte Islands are situated about 50 miles off the coast of British Columbia. The oregona females of these Islands have a higher mean value for length of elytra than have those from any other locality listed in Table 4, and the mean value for males is slightly less than those of Alta and Mount Timpanogos, Utah. However, the male samples from the Queen Charlotte Islands, Mount Timpanogos and Alta each are represented by fewer than 10 specimens and a more accurate comparison can be made with the females. Individuals from localities of high elevations in Utah, and Wyoming are scarcely broader than are those of Queen Charlotte Islands (see Table 8).

A relationship of body size with latitude or altitude is evident in many animal species other than Cicindela oregona. North American brown bears for example, increase in size as the latitude increases (Rausch 1963). This phenomenon has also been shown in many species of birds (Mayr 1942, 1963, Hamilton 1961). In insects, honey bees and two species of European Carabus vary in the same way (Mayr 1963, p. 326). New Guinea dragon flies have been found to increase in size in higher elevations also, as do populations of Cicindela oregona (Mayr 1963, p. 326). In ectothermal animals as a whole the largest body size may just as often be found in the warmest portion of a species range. Lindroth (1963) noted that in some Carabids of Newfoundland dwarf forms are frequently confined to high altitudes or marginal northern areas of the species range. Ball

(1959) observed that several species of the ground beetle genus Dicaelus were larger in southern areas of their ranges. Likewise the small, flightless grasshopper Melanoplus puer shows a general southward increase in size (Hubbell 1956). Mayr (1963) presents a review of evidence for the adaptive nature of geographic variation in which latitudinal and altitudinal changes are discussed in relation to geographic variation in body size.

Color pattern of elytra.- While body size of Cicindela oregona decreases from north to south the breadth of the white markings of the elytra increases. The diameter of the apical dot increases approximately 0.007 mm for each degree of latitude. Data on the expanse of elytral pattern, illustrated by the diameter of the apical dot, are presented in Table 6 for males and in Table 9 for females.

In the first route (A) from Alaska to New Mexico there is a slight uniform increase in apical dot size through British Columbia and Montana. In Fort Bridger, Wyoming the cline is steeper and continues to increase through Colorado to New Mexico. Fort Wingate, New Mexico is represented by individuals having a very wide apical dot with an average measurement of 0.78 mm. The difference between the mean values for males from Fort Wingate and those from Pecos, New Mexico is statistically significant, but this is not so for females. From a comparison between apical dot sizes both sexes from Hardy, Montana and from Helena and Lower Medicine Lake, Montana gave similar results.

A similar latitudinal increase in the diameter of the apical dot is evident in course (B) from Alaska to Arizona. There is a slight

decrease in the mean apical dot size of males in southern Idaho (this is not true for females) but the color pattern expands markedly in Utah. Populations with the widest apical dots are present in Floy, Utah, and Prescott and Globe, Arizona. A similar cline exists in the third path of population samples that extends from Alaska to Nevada.

Coloration.- The elytra, thoracic pleura, pronotum and, indeed, the entire body are subject to color variation in this species. The elytra may be brown, green, purple, blue and occasionally very dark brown that is almost black. The thoracic pleura are coppery, metallic blue, purple or green. Color of the pronotum and elytra is generally the same on each individual. Unicolored specimens occur throughout the species range in scattered localities and they are usually green, less frequently blue. In Arizona, southern Nevada, and southern New Mexico a green pronotum is usually associated with purple elytra. North of the limits of populations that have purple elytra the beetles are usually metallic blue-green ventrally and brown dorsally. Fig. 19 is a pie-graph map illustrating color variation of the elytra and thoracic pleura in populations in the northern portion of the range of oregona. Each "pie" represents a single population sample. Fig. 20 is a southwestern continuation of Fig. 19.

Color of thoracic pleura.- Coppery thoracic pleura are prevalent throughout northwestern British Columbia, Yukon Territory and Alaska. In Fig. 19 samples A (Tanana River, Alaska) to K (Helena, Montana) coppery thoracic pleura are most frequent, followed in number by metallic green, blue and purple, in that order. In Alaska, the Yukon Territory and northern British Columbia, only the coppery condition exists. In samples

D, E, F and G, in central British Columbia, individuals with metallic blue-green or purple thoracic pleura are present in low frequency. Southward, coppery thoracic pleura are prevalent in central British Columbia, on the eastern slopes of the Rocky Mountains in Alberta and Montana, and in eastern Idaho, Utah, Wyoming, Colorado, northeastern Arizona and northern New Mexico (see data for Fort Bridger, Wyoming and Jemez Springs, New Mexico in pictorialized scatter diagrams Figs. 25 and 27). In British Columbia (Fig. 19) coppery thoracic pleura are abruptly replaced by metallic purple thoracic pleura and this condition extends throughout southern British Columbia from the Pacific coast east to the Continental Divide. Of the individuals represented in samples L to U, only eight have coppery thoracic pleura in this region. Specimens with metallic green thoracic pleura are common in coastal populations of British Columbia and Washington, and also along the eastern ridge of the Rocky Mountains. This condition is less common in Oregon and California where metallic purple and metallic blue thoracic pleura are dominant (Fig. 20). Thoracic pleura of specimens in Owyhee County, Idaho (L) are predominantly metallic purple, also. Populations with thoracic pleura ranging from coppery to metallic purple through metallic blue and metallic green are found in northern Utah near Alta and southern Utah in the area of Zion National Park. Across southwestern United States from San Diego, California to Mountain Park, New Mexico, specimens with metallic purple thoracic pleura are most frequent.

Color of elytra.- Brown is the commonest color through most of the range of oregona. Brown color is entirely replaced by purple color in central Arizona, southern New Mexico and southern Nevada. This situation

is discussed in detail in the subspecies section. Populations that are highly variable in color of elytra occur throughout the range of this species. Such populations are on the Pacific coast from Alaska to southern California and almost all individuals with blue or green elytra exist in coastal localities (see Figs. 19, 20). Brown is most common, followed by green, and then blue. In Garibaldi Park, British Columbia, a very large proportion of specimens with blue elytra are present, while Vancouver and Victoria, British Columbia populations are made up mainly of individuals with green elytra. In Humboldt County, California and Port Orford, Oregon most of the specimens have brown elytra, and some members with green and blue elytra are also present. Likewise, a few individuals with blue and green elytra are present in San Francisco and in San Diego, California. Variation in elytral color is the rule in northern and southern Utah, where blue, green, and brown specimens are present.

Shelford (1917) studied color and color pattern of tiger beetles and he found, of the species studied in detail, the more brilliant colors occur in warm, arid localities, and extended markings in cooler regions. These findings apply only in part to oregona. In Arizona, New Mexico and southern Nevada, which are warm dry areas, specimens with bright metallic dorsal surfaces are prevalent but brilliant blue and green specimens of oregona also live along the Pacific coast from California to Alaska, and this is quite a humid zone. The markings of oregona are expanded in warmer localities and this condition contrasts with the results obtained by Shelford regarding pattern of elytra.

The pattern of variation.- Independent character changes have

resulted in discordant variation within C. oregona. Elytra are dark brown, generally, in the northern, eastern and western areas of the range but they are purple in the south, and very light brown in eastern Utah. In contrast, pleura usually blue to purple in the west and south, are coppery in northern and eastern portions of the range. In addition general body size decreases clinally from the north to south and also varies from higher to lower altitudes. Finally extent of white markings on elytra increases southward. Although recognition of subspecies in species that show discordant variation is controversial, (Inger 1961, also see section 2.29) I think it is useful to group into subspecies the population samples of oregona.

Maintenance of variation in this species appears to be largely dependent on geographical factors but may also be due to variation in the season of occurrence of adults. Mature specimens of my own and other collectors from boreal populations appear to be most plentiful for June, July, and August (based on specimen label information and personal collecting). This seems to be true for alpine populations in southern regions as well. Adult specimens from populations in desert areas of Utah, Arizona, and New Mexico have been collected from March to October inclusive. This suggests that they are common throughout this time but I do not believe so. Because C. oregona is riparian, size of populations, in arid southwestern regions, is likely to fluctuate with rain. Kendrew (1961) points out that rainfall is variable in these desert regions with a maximum in late summer and winter, and that the mountain ranges which rise on the southwestern plateau have rather more rain. It follows that activity peaks of desert populations probably do

not occur at the same time year after year but in different periods in relation to rainfall. Attempts to collect desert

forms during winter months have been unsuccessful. Perhaps they are most numerous during late summer - later than the peak of alpine populations. Such asynchronous number fluctuations effect a reduction in gene flow and thus maintain the variation between desert and alpine populations of the southwest.

Subspecies.- I recognize four subspecies of Cicindela oregona. I have followed the 75% rule in defining the group taxonomically (see Sec. 2.29, and Mayr, Linsley, and Usinger 1953). The differences between two or more populations in two or more characters is best illustrated by a pictorialized scatter diagram. Ten such diagrams and a locality map of population samples compared in the scatter diagrams serve as the graphical portion of this section (Figs. 21 - 31). Aggregates of populations can be readily distinguished from each other on the basis of one or more external characters. Males and females are treated separately. Generally five localities are represented in each diagram. Each locality is represented by ten specimens or less, and they have been selected randomly. Fifty specimen symbols are placed on a diagram. Extensive overlapping of symbols occurs if more than 50 are included, and this congestion obscures population sample character differences.

Key to the subspecies of Cicindela oregona

- | | | |
|---|--|-----------------|
| 1 | Thoracic pleura blue or purple..... | 2 |
| | Thoracic pleura coppery..... | 3 |
| 2 | Elytra purple; elytral pattern broad; pronotum green.... | <u>maricopa</u> |

- Elytra brown, green, blue or rarely purple; elytral pattern not broad; pronotum brown.....oregona
- 3 Elytra light brown; elytral pattern broad.....navajoensis
- Elytra dark brown; elytral pattern not broad.....guttifera

The nominate subspecies Cicindela oregona oregona ranges from southern British Columbia, in Canada, to southwestern California. It is present throughout Washington, Oregon, and California, except for the southeast portion of that state. The Continental Divide serves as the eastern limit in the north, from Banff, Alberta south to Yellowstone National Park, Wyoming. Further south oregona oregona is found as far east as Owyhee County, Idaho, western Nevada and finally near the southern portions of the Sierra Nevada Mountains in California (Fig. 18). A combination of semi metallic green, blue or brown elytra with metallic purple or blue thoracic pleura is characteristic of this subspecies. Individuals with green elytra are numerous in or near the above localities. I can only speculate about the reasons for the scattered occurrence of these blue and green individuals along the Pacific coast. They may be evidence of a blue form that was once widespread in these coastal regions, but then the range was invaded by a more vigorous stock, characterized by the possession of brown elytra. Whenever these two aggregates of populations came into contact introgression took place and the presence of green individuals interpreted as hybrids, mark what once were zones of contact. In more southern locations these green and blue forms have been all but completely replaced by the brown condition. On the other hand they may be recent phenotypes whose gene complex originated in southwestern British Columbia when the blue phenotypes were relatively common. Another possibility

is that the green and blue forms might be ecophenotypes. Although Shelford observed that Cicindela tranquebarica is green on the coasts and coastal mountains and also that in Cicindela scutellaris green forms and some blue were most common along the Atlantic coast (Shelford 1917), he did not believe that this was the result of direct influence of the environment on the phenotypes.

The subspecies o. oregona comes in contact with o. guttifera LeConte in southern British Columbia and along the slopes of the Rocky Mountains from Banff, Alberta to Yellowstone National Park, Wyoming. Many specimens that appear to be hybrids are present in areas of contact of these two subspecies, and such are distinguished by their metallic green thoracic pleura (Fig. 19).

In San Diego, California a highly variable group of populations is present (Fig. 20), for in this area specimens typical of both o. oregona and o. maricopa occur. This situation could be the result of maricopa genes infiltrating the more numerous oregona population in the region (Figs. 22, 23). Only five phenotypically maricopa specimens are known from the San Diego area.

Cicindela o. guttifera ranges the Rockies from Fort Yukon, Alaska to northern New Mexico (Fig. 18). In Alaska and north and central British Columbia, guttifera ranges from the Pacific coast to the eastern slopes of the Rockies but continues southward in a very narrow zone to northern New Mexico. This subspecies also occurs in northern and central Utah. Coppery thoracic pleura and brown elytra that have a metallic lustre characterize it. I have already mentioned that hybridization takes place

between oregona guttifera and oregona oregona in much of eastern Idaho and western Montana; and intermediate specimens with metallic green sides are not uncommon in northern and central Utah where they are distributed through oregona guttifera populations. In southwestern Utah a highly variable series of populations occurs, consisting of individuals ranging from typical guttifera to typical maricopa. This region is undoubtedly a melting pot of these two subspecies (Figs. 24, 25). It may be argued that this variation is a result of hybridization between oregona and maricopa and not as above. This is not likely since at the present time oregona is uncommon in eastern Nevada and it is not abundant in Utah, but may have contributed to this variation during pluvial times.

The range of Cicindela o. navajoensis and guttifera come very close in northwestern New Mexico (Fig. 18). Navajoensis is relatively small in size and has much lighter brown elytra and broader pattern of elytra than guttifera. Like the latter, navajoensis has coppery thoracic pleura. A color character gradient occurs from Kayenta, Arizona to Jemez Springs, New Mexico through an intermediate locality, Fort Wingate, New Mexico. Color of the elytra in Kayenta is light brown, dark brown in Jemez Springs and intermediate in Fort Wingate. Figs. 26 and 27 illustrate differences and similarities based on lengths and widths of elytra and the apical dot. Fort Wingate specimens are intermediate on the basis of these characters as well.

The geographical ranges of oregona and navajoensis are not in contact; their morphological relationships are demonstrated in Figs. 28 and 29.

In southeastern Arizona and southwestern New Mexico are variable populations that consist of individuals morphologically between navajoensis and maricopa (Figs. 30, 31). The members of these groups are generally smaller in body size than maricopa and larger than navajoensis. Their elytra are mainly purplish brown. The Fort Wingate sample in Figs. 30 and 31 is not pure navajoensis but is intermediate between navajoensis and guttifera (Figs. 26, 27). Thus the specimens appear as intermediates between navajoensis and maricopa in Figs. 30 and 31.

The fourth subspecies is o. maricopa. Specimens of this subspecies have brilliant purple elytra, brown to metallic green pronota, and metallic purple thoracic pleura. Maricopa is distributed sparsely through southern California, southeastern Nevada, and southern New Mexico, but it is common in central and southern Arizona (Fig. 18). California "maricopa" may be a minor element in predominantly o. oregona populations and if so they are maricopa in a typological sense only. The morphology of this and other subspecies of Cicindela oregona has been compared in the above section.

History of distribution and subspeciation

Distribution of C. oregona is restricted to western United States and Canada bounded by Alaska, southern California, Arizona and New Mexico and the Rocky Mountains. Within this area four geographically distinct groups of populations exhibit boundaries that are generally barriers such as deserts and mountain ranges (Fig. 18). All population samples of these subspecies that I have examined, have been collected in the above described range of C. oregona. I have seen two maricopa specimens,

however, that are labelled "Texas", but specific localities are not given. They could have been collected in western Texas near maricopa localities in New Mexico. Because the total range of C. oregona is well marked and no populations occur in remote regions outside of the described range it appears highly likely that subspeciation took place somewhere in western North America.

Before discussing further the questions of how and when formation of subspecies occurred in oregona it should be emphasized that determination of evolution of a subspecies without a fossil record is a highly speculative matter. Fossils are not available, and even if they were it would be impossible to determine all of the subspecific development in oregona because color is not preserved in fossils. As a result indirect evidence must be used. This is provided by a consideration of the effects Pleistocene climatic changes may have had on bringing about subspeciation in oregona.

It seems that isolation of groups of populations of oregona occurred at different times in relation to climatic changes; that is, not all groups were isolated simultaneously. In southern portions of the species range populations were separated from each other during interglacial periods because of the formation of deserts.

Northern incipient subspecies were probably separated during glacial times.

Because oregona is riparian, regions void of river systems or lakes act as geographic barriers. The great deserts of southwestern United States prove to be barriers (Fig. 18), and distribution of subspecies is

closely linked to wet and cool areas. Consequently it may be deduced that isolation and subsequent genetic divergence of southern populations took place when southwestern United States was largely desert; perhaps during the last interglacial period. During glacial times, on the other hand, river systems were very extensive and many lakes occurred in the southwest (Blackwelder, 1948, and Hubbs and Miller, 1948). In these regions populations were undoubtedly dispersed most widely in glacial times and presumably gene flow was uninhibited.

Conversely, partitioning of incipient subspecies that existed in northern regions of this species range probably occurred during glacial times, while range expansions occurred in interglacial periods. In glacial periods great ice masses moved down from the north, scarcely crossing the Canadian-American border in the west. These undoubtedly obstructed gene flow between aggregates of populations on the eastern portions of the Rockies and populations further west by way of northern United States and southern Canada. For example if an ice mass was at present established across the northwest *C. oregona* and *C. guttifera* would be spatially isolated because they normally intergrade in Idaho, Montana, southern Canada and northern Utah. Similarly glaciers that developed throughout most of the major mountain ranges in glacial times must have reduced east-west gene flow further south.

Interpretation of present distribution of the subspecies and knowledge of the events of the Pleistocene epoch suggests the following course of subspeciation (see Fig. 32). Two subspecies of *C. oregona* *oregona* and *guttifera* as they are defined in this text, were formed in part during the Iowan glacial stage. A uniform "protooregona" species

was distributed across northwestern United States and southwestern Canada prior to this period. With the advent of the Iowan ice mass and glacier formation all "protooregona" populations north of the Canadian-American border were probably annihilated, at least as a result of cooling, and two large populations were isolated on either side of the Continental Divide. During this period race A and race B came into being, race B east of the Continental Divide and race A in the west. Both subspecies were more widespread in the south than they now are. Race B occupied all of the Great Basin, Arizona and regions west of the Sierra Nevada. Geographic variation was pronounced in this race with brown forms predominant in the north and blue in the south. Restricted to regions east of the Continental Divide in the north, race A extended southward into Colorado and New Mexico then swung northward through lower elevations in northwestern New Mexico and northeastern Arizona and eastern Utah. This was the situation when the Prairie interglacial stage began.

Much partitioning and spatial isolation between southern populations took place during the Prairie interglacial as a result of vast desert formation. During this stage southern, blue populations of race B subspeciated to maricopa and western populations to oregona. Race A forms became navajoensis and guttifera. Distributions of aggregates of populations shrank and assumed geographic areas approximately where the subspecies of C. oregona now exist. C. oregona blue populations in the south were pinched off from their counterparts in the northwest by deserts where the Mohave Desert and Great Basin are now located. In Utah navajoensis populations remained partially isolated from populations in Colorado by the intervening Rocky Mountains, and were isolated from the

effects of the oregona blue forms in the southwest. In the north oregona and guttifera reinvaded regions south of the retreating ice mass in northern United States and Canada and formed marked hybrid areas wherever their ranges came into contact.

Southern hybrid zones were primarily formed in the Wisconsin glacial period as a result of expanding subspecific ranges. Pluvial lakes that were reestablished in desert areas along with revived river systems served as routes for expanding ranges and intergradation was widespread. In the north oregona and guttifera were isolated from each other as in the previous glacial period.

Since the Wisconsin ice age ranges of subspecies have shrunk in the southwest. A few specimens phenotypically maricopa have been found in southern California but true maricopa is abundant only in central Arizona. This implies that maricopa once was more extensively distributed. On the other hand oregona and guttifera ranges appear to be expanding in the north. Furthermore distribution of hybrids in the southwest has recently been reduced in area. Evidence of this is available in southeastern Arizona and southwestern New Mexico. Pure maricopa specimens along with maricopa x navajoensis hybrids exist in these regions, but pure populations of navajoensis are located in northeastern Arizona and northwestern New Mexico, many miles away from where the hybrids are found.

Cicindela duodecimguttata and C. o. guttifera may have formed hybrid populations along the southeastern foothills of the Rocky Mountains during Pleistocene times. Such hybrid populations were probably subject to extreme fluctuation as in Nordegg, Alberta at the present time (see Sec. 5.0).

These unstable intermediate forms had no profound effect on the parental forms.

This discussion presents one interpretation of subspeciation in C. oregona that is based on knowledge of distribution pattern of C. oregona and Pleistocene events in southwestern United States. Undoubtedly other explanations of the available data are possible.

Distribution

I examined 6,073 specimens. Several specimens appeared to be labelled wrongly. Two maricopa specimens were labelled Fort Garland, Castilla County, Colorado. Fort Garland is well into guttifera territory beyond the northern limits of maricopa at that longitude. Another maricopa specimen has an identification label with Sonoma County, California written on it. This appears to be unlikely since Sonoma County is in northwestern California approximately seven hundred miles north of the maricopa specimens in San Diego. Five specimens of o. guttifera were labelled as being collected in Santa Rita Mountains. This is unlikely but not impossible since these specimens could represent an isolated relict population which has survived in these mountains since the end of the Pleistocene.

Cicindela o. oregona LeConte. Canada. BRITISH COLUMBIA:

Abbotsford, 9; Agassiz, 25; Ainsworth, 6; Aiyansh, 1; Atbara, 7; Bear Foot, 1; Cherrierville, 2; Chilliwack, 2; Columbia Lake, 1; Comox, 8; Copper Mine, 2; Courtenay, 4; Cranbrook, 3; Creston, 139; Duncan, 3; Duncan and Cowichan Lake, 1; Elk Lake, 1; Fairmont, 1; Field, 1; Fraser River, 1; Gabriola, 2; Garibaldi Park, 29; Golden, 1; Goldstream, 1; Harrison, 2; Hatzic, 20; Hope, 1; Howser, 7; Huntingdon, 15; Kamloops, 3;

Kaslo, 8; Keremeas, 2; Likely, 1; Lillooet, 9; Lynn Valley, 1; Lytton, 2; Mabel Lake, 2; MacGillivray, 53; McIntyre Creek, 1; Merritt, 22; Miracle Beach, 60; Misson City, 20; Nanaimo, 1; Nanoose, 5; North Bend, 4; Okanagan Lake, 1; Oliver, 61; Osoyoos, 2; Peachland, 3; Pender Harbour, 5; Penticton, 3; Point Grey, 2; Powell River, 2; Radium, 3; Read Bay, 4; Riodel, 11; Rock Creek, 7; Salmon Arm, 3; Sanca, 12; Shuswap Falls, 1; Stillwater, 1; Summerland, 4; Tood Inlet, 1; Trinity, 1; Vancouver, 79; Vancouver Island, 5; Vaseaux Lake, 13; Vernon, 42; Victoria, 18; White Lake, 2; Windemere, 1; Wynndel, 8.

United States. CALIFORNIA: Alameda County: 11; Berkley, 17; Oakland, 10. Alpine County: 7; Soda Springs, 1. Butte County: Chico, 4; Chico Creek, 1; Oroville, 2. Calaveras County: Big Trees, 6; Mokelumne Hill, 7. Contra Costa County: Antioch, 32. Del Norte County: Crescent City, 6; Terwah, 1. Eldorado County: Bijou, 2; Desolation Valley, 1; Echo, 1; Fallen Leaf Lake, 1. Fresno County: Cedar Grove, 1; Coalinga, 12; Fresno, 3; Huntington Lake, 15; Macy Mines, 1; Stevenson Creek, 1. Glenn County: Elk Creek, 2. Humboldt County: Blue Lake, 2; Blairs Ranch, 3; Bridgeville, 28; Bridgeville (15 miles east), 5; Eel River, 1; Eureka, 9; Ferndale, 2; Fort Seward, 26; Hoopa, 44; Miranda, 29; Pepperwood, 1; Jct. Redwood Creek and Rte. 299, 12; Scotia, 3; Trinidad, 1; Trinidad (5 miles south), 25; Van Duzen River, 2; Willow Creek, 1. Inyo County: Bigpine (2 miles west), 12; Bigpine (2 miles north), 20; Bishop, 2; Lone Pine, 11; Olancho, 18; Owens Lake, 3. Kern County: Bakersfield, 2; Bakersfield (4 miles east), 9; Cottonwood Creek, 1; Isabella, 1. Lake County: Borax Lake, 5; Hullville, 3; Lake Pillsbury, 8; Lakeport, 2;

Lower Lake, 1. Lassen County: Facht, 1; Goumaz, 4; Madeline, 1; Pine Creek, 1; Susanville, 1. Los Angeles County: Burbank, 2; Covina, 1; Crystal Lake, 1; El Monte, 3; Gabriel Mountains, 1; Los Angeles, 57; Palmdale, 1; Point San Pedro, 5; San Pedro, 1; Santa Monica, 10; Tropico, 1. Madera County: Jackass Meadow, 1; Madera, 1; North Fork, 2; Placer Station, 2. Marin County: Bon Tempe, 4; Dillon Beach, 6; Inverness, 1; Lagunitas, 1; Mill Valley, 1; Point Reyes Station, 4. Mariposa County: Mariposa Grove, 1; Yosemite National Park, 22; Yosemite Valley, 1. Mendocino County: Caspar, 1; Eagles Nest, 1; Fort Bragg, 1; Littleriver, 2; Philo, 1; Yorkville, 3. Merced County: Lake Merced, 7; Los Bonos, 1; Santa Rita, 2. Modoc County: Cedarville, 2; Goose Lake, 1; Lake City, 1. Mono County: Coleville, 1; Lake Mary, 5; Mono County, 13; Mono Lake, 6; Sonora Pass, 2; Topaz Lake, 8. Monterey County: Bradley, 1; Carmel, 34; Pacific Grove, 1; Salinas River, 6; Soledad, 2; Stone Canyon, 4. Nevada County: Norden, 2; Soda Springs, 1; Truckee, 7. Orange County: Anaheim, 5; Laguna Beach, 2. Placer County: Brockway, 2; Dutch Flat, 2; Lake Tahoe, 75; Summit, 1. Plumas County: Bucks Ranch, 20; Clio, 1; Meadow Valley, 1; Near Twain, 1; Quincy (4 miles west), 2; Tobin, 1; U.S. Alt. 40 (2.1 miles W. U.S. 395), 30; Walker Mine, 1. Riverside County: Hemet Res., 8; Idyllwild, 20; Indio (30 miles north), 2; Lake Elsinore, 2; Riverside, 12; San Jacinto Mountains, 13; Temecula, 1; White Water Canyon, 2. Sacramento County: Sacramento, 19. San Bernadino County: Big Bear, 7; Big Bear Valley, 1; Cajon, 3; Cajon Pass, 1; Colton, 21; Victorville, 13; Yermo, 1. San Diego County: Descanso, 1; Guatay, 1; Julian, 3; Mesa Grande, 5; Oceanside, 1; Poway, 1; Warner Springs, 1. San Francisco County: San Francisco, 22. San Joaquin County: Stockton, 7. San Luis Obispo County: Paso Robles, 1; Pismo Beach, 3.

San Mateo County: Salada Beach, 7. Santa Clara County: Los Gatos, 1; Palo Alto, 2; San Jose, 3. Santa Cruz County: Santa Cruz, 4; Soquel Basin, 3. Santa Cruz Island, 13. Shasta County: Bumpas Hell, Lassen National Park, 5; Castella, 2; Hat Creek, 3; Hat Lake, 1; Manzanita Lake, 4; Mount Lassen, 3; Redding, 3; Shasta National Forest, 3; Shasta Springs, 11; Viola, 1. Sierra County: Sierraville, 9; Yuba Pass, 1. Siskiyou County: Dillon Creek, Klamath River Valley, 21; Dunsmuir, 4; Gottville, Klamath River Valley, 24; Etna, 3; McCloud, 10; Tule Indian Reservation, 1. Solano County: Dixon, 1. Sonoma County: Cloverdale, 15; Duncans Mills, 1; Santa Rosa, 4. Stanislaus County: Patterson, 1. Sutter County: Yuba City, 5. Tehama County: San Bernardino Mountains, 1. Trinity County: Douglas City, 14; Jct. Mad River, Rt. 36, 37. Tulare County: Burton Meadow, 1; Kaweah, 2; Lemoncove, 6; Lloyd Meadow, 1; Sequoia National Park, 8. Tuolumne County: Hardin Flat, 12; Pinecrest, 1; Strawberry Resort, 11. Yolo County: Davis, 6. Localities of unknown counties: Alta, 1; Asilomar, 1; Bear Lake, 1; Bentons Crossing, 3; Big Dalton Dam, 6; Borego, 1; Bryson 1; Carrville, 14; Charity Valley, 1; China Flat, 2; Colony Mill, 1; Ebbet Pass, 1; El Mirador, 1; Fort Ross, 3; Giant Forest, 2; Hackamore, 5; Hartsooks, 2; Hickey Grove, 7; Hueneme, 1; Ingleside, 2; Kings River, 11; Lake Clay, 1; Lassen Creek, 1; Leech Lake Mountain, 6; Marble Bridge, 1; Marwedel, 1; Miami, 1; Mount Tallac, 1; Panoche Canyon, 1; Paradise Springs, 1; Pohono, 3; Poloa, 4; Poso Creek, 1; Redstone, 2; Sandflat, 6; San Juan, 1; San Pedro Valley, 15; Shaver, 1; Sheep Creek, 1; Silliman, 1; Simmler, 1; Sylvania, 1; Tassajara, 5; Towie, 1; Tunnel R. S., 1; Vera Lake, 1; Waddell Beach, 2; Walker, 6.

IDAHO: Ada County: 6; Boise, 2. Blaine County: Carey, 1. Boise County: 13. Bonner County: Hope, 1; Priest Lake, 1; Priest River, 5; Sandpoint, 1.

Boundary County: Selway Falls (2.5 miles south), 1. Canyon County: 8; Nampa, 1. Elmore County: Atlanta, 2. Gooding County: Hagerman, 1. Idaho County: 4. Jerome County: Jerome, 1. Kootenai County: Cataldo, 1; Coeur d'Alene, 5; Medimont, 1. Latah County: Moscow, 7; Troy, 1. Nez Perce County: Lake Lowell, 2; Lewiston, 5. Owyhee County: Homedale, 1; Cwyhee County, 62. Power County: American Falls, 1. Shoshone County: Wallace, 1. Valley County: Cascade, 1; McCall, 1. Valley County: 20.

NEVADA: Churchill County: Fallon, 3. Douglas County: Lake Tahoe, 1; Minden, 24. Elko County: Elko, 4; Lamoille, 1. Mineral County: Hawthorne, 10; Walker Lake, 45. Ormsby County: Carson City, 3. Pershing County: Lovelock, 1. Washoe County: Gerlach, 2; Mount Rose, 1; Nixon, 1; Pyramid Lake, 18; Reno, 19; Verdi, 1. White Pine County: McGill, 1.

OREGON: Baker County: Pine Creek, 1; Richland, 1. Benton County: Corvallis, 8; Umatilla, 10. Clackamas County: Estacada, 4. Clatsop County: Cannon Beach, 1; Clatsop Beach, 2. Columbia County: Rainier, 1. Coos County: Cape Arago, 2; Charleston, 16; Coos Bay, 4; Coos Head, 1. Curry County: Humbug Mountain, 6; Port Orford, 12. Grant County: John Day George, 2. Harney County: Frenchglen, 8; Malheur Lake, 15; P. Ranch, 1; Steens Mountains, 15. Hood River County: Hood River, 8; Mount Hood, 2; Parkdale, 1. Jackson County: Medford, 10; Rogue River, 1; Ruch, 2. Josephine County: Grants Pass, 5; Hells Gate Bridge, 2; Murphy, 1. Klamath County: Crater Lake, 2; Klamath Lake, 6; Lake O Woods, 3; Pinehurst (21.9 miles east), 1. Lake County: Lake Albert, 12; Paisley, 3. Lane County: Eugene, 13; Florence (3 miles north), 13. Lincoln County: Depoe Bay, 2; Newport, 6; Waldport, 5; Yachats (5 miles south), 5. Linn County: Cascadia, 1. Malheur County: Sucker Creek Canyon, 1. Marion County: Detroit, 1. Multnomah County: Portland, 9. Tillamook County: Pacific City, 1;

Tillamook, 1; Woods, 4. Umatilla County: Echo, 2; Hermiston, 3; Meadow Lake, 1. Wasco County: The Dalles, 7; Tygh Valley, 1. Yamhill County: Dayton, 6; McMinnville, 4. Localities of unknown counties: Alvord Hot Springs, 3; Blitzen Valley, 1; Boiler Bay, 5; Buell, 1; Devils Lake, 1; Durnep, 2; McNair Lake, 1; Moffat Mead, 1; Ocean Park, 1; Oregon (south east), 3; Santiam, 4; Sparks Lake, 1; Whitman, 2. UTAH: Salt Lake County: Alta, 13; Brighton, 1. Utah County: American Fork Canyon, 9. WASHINGTON: Adams County: Othello, 7. Asotin County: Asotin, 1; Clarkston, 1. Benton County: Paterson, 1. Chelan County: Leavenworth, 1; Peshastin, 4; Stehekin, 1; Wenatchee, 5. Clallam County: Port Angeles, 1. Columbia County: Huntsville, 3. Douglas County: Moses Coulee, 3. Franklin County: Kahlotus, 2; Pasco, 1. Grant County: Beverly, 3; Goose Lake, 1; Moses Lake, 1; Stratford, 9. Grays Harbor County: Moclips, 3. Island County: Coupeville, 1; Whidby Island, 53. Jefferson County: Port Townsend, 17. King County: Auburn, 2; Bothell, 4; Cedar Mountain, 5; Maple Valley, 3; Renton, 13; Seattle, 80; Selleck, 1; Snoqualmie, 1. Kitsap County: Bremerton, 49; Chico, 34; Gorst, 120; Keyport, 1; Kingston, 13; Manchester, 1. Kittitas County: Ellensburg, 2; Vantage, 12. Klickitat County: Goldendale, 1; Goldendale (32.3 miles north), 22. Lewis County: Chehalis, 2. Lincoln County: Sprague, 2. Mason County: Lake Cushman, 1; Spillman, 2. Okanogan County: Brewater, 5. Pacific County: Bay Center, 4; Ilwaco, 1; Long Beach, 1; Nahcotta, 2; North Cove, 1; Ocean Park, 3. Pend Oreille County: Newport, 1. Pierce County: Buckley, 1; Chinook Pass, 3; Mount Rainier, 1; Sumner, 1; Tacoma, 4. San Juan County: False Bay, 1; Friday Harbor, 9. Skagit County: Anacortes, 18. Snohomish County: Cicero, 2; Darrington, 6; Everett, 3; Index, 4; Sulton, 1;

Verlot, 8. Spokane County: Medical Lake, 4; Spokane, 13. Stevens County: Wellpinit, 1. Thurston County: Olympia, 1; Tenino, 5. Walla Walla County: Dixie, 10; Lowden, 1; Touchet, 27; Wallula Gap, 1. Whatcom County: Bellingham, 1; Mount Baker, 2. Whitman County: Almota, 3; Pullman, 30; Wawawai, 11. Yakima County: Toppenish, 4; White Swan, 1; Yakima, 2. Localities of unknown counties: Barkerville, 1; Blue Mountains, 1; Central Ferry, 1; Clifton, 1; Ginko State Park, 2; Half Moon Lake, 2; Lyons Ferry, 9; Neppel, 10; Paha, 5; Pot Holes, 2; Saratoga Beach, 5; Silverton, 1; Skating Lake, 1; Stillaguamish, 2; Tolsak, 1.

Cicindela oregona guttifera LeConte. Canada. ALBERTA:

Kootenay Plains, 14. BRITISH COLUMBIA: Aiyansh, 1; Blue River, 1; Bucks Bar, 1; Cariboo Road (mile 185), 2; Glenora, 1; McNab Creek, 1; Juskalta, 6; Massett, Queen Charlotte Islands, 10; Moresby Camp, Queen Charlotte Islands, 9; Queen Charlotte City, 1; Stickeen River, 1; Tlell, Queen Charlotte Islands, 9. NORTHWEST TERRITORIES: Fort Good Hope, 2; South Nahanni River, 1. YUKON TERRITORY: Kirkman Creek, 1; Watson Lake, 6.

United States. ALASKA: Eagle, 3; Fairbanks, 5; Fort Yukon, 11; Haines, 12; Tanana River, 27; Valdez, 4; Yukon River, 1. COLORADO: Alamosa County: Alamosa, 3. Boulder County: Boulder, 5; Jamestown, 2; Lyons, 1; Pinecliffe, 2. Chaffee County: Buena Vista, 2; Salida, 3. Clear Creek County: Georgetown, 1. Conejos County: Cumbres Pass, 4; La Manga Pass, 4. Douglas County: Larkspur, 2. El Paso County: Cascade, 1; Colorado Springs, 6; Colorado Springs (10 miles south), 6; El Paso County: 2; Manitou Springs, 5. Freemont County: Coalcreek, 1. Garfield County: Glenwood Springs, 1. Grand County: Big Muddy Creek, 1; Fraser, 1.

Jefferson County: Golden, 7. La Plata County: Electra Lake, 1. Larimer
 County: Estes Park, 25; Fort Collins, 6. Las Animas County: Trinidad,
 26. Mineral County: Creede, 4; Wolf Fall Creeks, 2. Ouray County: Ouray,
 1. Park County: Colorado Springs (50 miles west), 4. Pitkin County: Aspen,
 4. Saquache County: Great Sand Dunes National Monument, 4. Teller County:
 Victor, 1. Localities of unknown counties: Berkley, 1; Gothic, 1;
 Rockwood, 2; South Fork, 1; Thomasville, 1. NEW MEXICO: Bernalillo
 County: Albuquerque, 1. San Doval County: Bernalillo, 1; Jemez
 Mountains, 17; Jemez Springs, 47; Jemez Springs (9 miles north), 73;
 Jemez Springs (10 miles north), 43. San Miguel County: Beulah, 2. Santa
 Fe County: Pecos River, 17; Santa Fe (3 miles east), 2. Localities of
 unknown counties: San Antone, 1. UTAH: Beaver County: Beaver Creek, 1.
 Cache County: Logan, 3. Juab County: Levan (5 miles south), 1. Millard
 County: Lynndyl, 1. Piute County: Piute Reservoir, 18. Rich County:
 Bear Lake, 1. Salt Lake County: Mount Dell Creek, 1; Parley Canyon, 3;
 Salt Lake City, 18; Salt Lake County, 24. Sampete County: Sevier Bridge
 Reservoir, 21. Summit County: Echo, 2; Park City, 3. Tooele County:
 Stockton, 15. Uintah County: Power Plant, 2. Utah County: Mount
 Timpanogos, 20; Payson, 1; Provo, 17; Provo Canyon, 26; Utah Lake,
 19. Wasatch County: Soldier Summit, 3; Wasatch County, 2. Weber County:
 Ogden, 13; Ogden (30 miles east), 8. Localities of unknown counties:
 Emigration, 1; Hillneck Canyon, 1; Kawara, 6; Red Butte Canyon, 1; Salt
 Creek Canyon, 1; Silver Lake, 5; Vineyard, 26. WYOMING: Albany County:
 Centennial, 1; Jelm, 88. Carbon County: Baggs, 2; Saratoga (8 miles south),
 24. Fremont County: Lander, 1. Lincoln County: Labarge (11 miles south),
 21. Sublette County: Big Sandy Reservoir, 11; Half Moon Lake, 11;
 Sweetwater River, 2. Sweetwater County: Green River, 54; Green River (26

miles south), 6; Old Ford on Green River, 34; Sweetwater County, 7.

Uinta County: Fort Bridger, 64; Lyman, 4.

Cicindela oregona maricopa Leng. United States. ARIZONA:

Coconino County: Grand Canyon, 1. Gila County: Globe, 56; Roosevelt

Lake, 4; San Carlos, 1; Sierra Ancha Mountains, 7. Graham County:

Bylas, 8. Greenlee County: Clifton, 9. Maricopa County: Phoenix, 25;

Tempe, 1. Pima County: Tuscon, 5. Pinal County: Pinal Mountains, 7.

Yavapai County: Cottonwood, 1; Haslampa, 3; Prescott, 266. Localities

of unknown counties: Bad Creek Canyon, 1; Bradshaw Mountains, 1; Mogollon

Mountain, 1; Oak Creek Canyon, 2. CALIFORNIA: Los Angeles County, 1.

San Bernardino County: Barstow, 1. NEVADA: Lincoln County: Caliente,

13; Meadow Valley, 1. NEW MEXICO: Otero County: Cloudcroft, 2; Mountain

Park, 15. UTAH: Iron County: Cedar City Canyon, 2.

Cicindela oregona navajoensis Van Dyke. United States.

ARIZONA: Navajo County: Betatakin, 9; Kayenta, 25; Navajo Mountain, 6.

Moffat County: Echo Park, 2; Massadona, 4. Montezuma County: Four

Corners, 4. UTAH: Grand County: Floy, 40; San Juan County: Blanding

(10 miles west), 4; National Monument, 1; Navajo Mountain Trading Post, 7.

Cicindela oregona oregona x Cicindela oregona guttifera.

Canada. ALBERTA: Banff, 52; Laggan (Lake Louise), 22; Waterton Park, 5.

BRITISH COLUMBIA: Athalmer, 24; Canal Flats, 8; Cinema, 7; Fernie, 25;

Fort Fraser, 13; Kootenay National Park, 6; Moyie, 2; Terrace, 35; Wasa,

7; Yoho National Park, 17.

United States. IDAHO: Bannock County: Pocatello, 7. Bear Lake

County: Bear Lake, 119; Bloomington Lake, 10. Franklin County: Franklin

Basin, 11. Fremont County: Parker, 2. Lemhi County: Salmon (21 miles north), 6. MONTANA: Cascade County: Great Falls, 2. Flathead County: Hungary Horse, 11; Kalispell, 1. Gallatin County: Bozeman, 2; Gallatin County, 2; Gallatin River and Highway 10, 14; Lake Hebgen, 12; Missouri River (headwaters), 2; Three Forks (3 miles west), 13. Glacier County: Lower Medicine Lake, 66. Lewis and Clark County: Craig, 14; Helena, 50; Hardy (15 miles south west), 33. Lincoln County: Troy, 1. Missoula County: Frenchtown, 1. Park County: Gardiner (5 miles north), 86. Ravalli County: Darby, 2; Florence, 2; Hamilton, 3; Ravalli County, 2; River Bottoms, 10; Skalkaho, 1. Sanders County: Whitepine, 1. Silver Bow County: Butte, 1. Localities of unknown counties: Beaver Creek, 8; Bitter Root Mountains, 2; Lost Horse Canyon, 1; Marias River, 2; Stickney Creek, 34. WYOMING: Teton County: Black Rock Creek, 4; Grand Teton National Park, 13; Hoback Canyon, 3; Jackson Hole National Monument, 27; Moran (38 miles east), 46. Yellowstone National Park, 140.

Cicindela oregona oregona x Cicindela oregona maricopa.

United States. CALIFORNIA: San Diego Diego County: San Diego, 45.

Cicindela oregona guttifera x Cicindela oregona maricopa.

United States. UTAH: Beaver County: Beaver (4 miles east), 11; Beaver Canyon, 6; North Creek, 1. Iron County: Burkshire, 1; Cedar City, 9; Iron Springs, 2; Parowan (5 miles south east), 7; Parowan Canyon, 12. Kane County: Glendale, 1; Kanab, 1; Orderville, 2. Washington County: Bellvue, 2; Pine Valley, 2; Pintura, 3; Saint George, 8; Santa Clara, 3; Zion National Park, 26. Localities of unknown counties: Mount Meadows, 1; Weeping Rock, 1.

Cicindela oregona guttifera x Cicindela oregona navajoensis.

United States. COLORADO: Mesa County: De Beque, 4; Palisade, 7. NEW MEXICO: McKinley County: Fort Wingate, 33. San Juan County: Farmington, 3. UTAH: Uintah County: Dinosaur National Monument, 1; Vernal, 12.

Cicindela oregona navajoensis x Cicindela oregona maricopa.

United States. ARIZONA: Apache County: White Mountains, 8. Cochise County: Chiricahua Mountains, 2. Navajo County: Carrizo, 8; Cibique Creek, 2. NEW MEXICO: Catron County: Luna, 5. Brant County: Silver City, 6.

TABLE 4. - Data on the variation in length of elytra of male Cicindela
oregona.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
A,B,C	Alaska									
	Tanana R.	63.00	1500	16	6.65-7.73	7.26	0.09	0.35	4.75	
A,B,C	British Columbia									
	Terrace	54.31	223	19	6.70-7.60	7.24	0.06	0.25	3.49	
	Q.Ch. Islands	53.00	0-4100	7	6.81-7.70	7.34	-	-	-	
	Oliver	49.10	2143	36	6.35-7.92	7.13	0.06	0.36	5.02	
A	Montana									
	Low.Medicine Lake	48.30	5000	44	6.91-7.62	7.16	0.03	0.18	2.49	
	Hardy	47.11	3500	17	6.28-7.38	6.96	0.08	0.33	4.80	
	Helena	46.35	4160	28	6.61-7.50	7.06	0.05	0.26	3.71	
	Gardiner	45.03	5800	40	6.27-7.85	7.24	0.05	0.32	4.36	
A	Wyoming									
	Yellowstone N.P.	44.30	7000	77	6.13-7.98	7.19	0.04	0.38	5.33	
	Jackson Hole N.M.	43.50	6800	19	6.21-7.79	7.23	0.08	0.34	4.67	
	Moran	43.52	6800	27	6.52-8.13	7.22	0.05	0.26	3.57	
	11 miles S.									
	Labarge	42.15	6600	16	6.06-7.63	7.01	0.11	0.42	6.05	
	27 miles S.									
	Labarge	42.14	6600	14	6.59-7.65	7.03	0.08	0.29	4.18	
	Green River	41.33	6100	30	6.13-7.44	6.91	0.07	0.37	5.31	
	Fort Bridger	41.19	6657	38	6.46-7.77	7.21	0.05	0.31	4.30	
	Saratoga	41.28	6790	15	6.75-7.54	7.09	0.06	0.23	3.23	

TABLE 4. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A	Jelm	41.03	7500	46	6.21-7.66	7.01	0.04	0.28	3.95
	Colorado								
	Estes Park	40.24	7547	12	6.32-7.32	7.02	0.08	0.27	3.85
A	Trinidad	37.11	5999	16	6.23-7.03	6.69	0.06	0.25	3.75
	New Mexico								
	Jemez Springs	35.45	6195	78	6.10-7.45	6.86	0.03	0.29	4.23
	Pecos & Beulah	35.34	7000	10	6.40-7.18	6.73	0.09	0.27	4.01
	Fort Wingate	35.30	6997	13	6.25-7.10	6.66	0.08	0.27	4.05
B,C	Idaho								
	Valley County	45.00	-	7	6.28-7.56	7.01	-	-	-
	Owyhee County	42.30	-	22	6.15-7.61	7.03	0.09	0.40	5.66
	Bear Lake	42.05	5924	61	6.23-7.92	7.02	0.05	0.38	5.34
B	Utah								
	Ogden	41.14	4296	10	6.40-7.75	7.04	0.14	0.43	6.15
	Salt Lake City	40.45	4354	20	6.50-7.73	7.26	0.08	0.35	4.82
	Alta	40.36	8585	2	7.34-7.55	7.45	-	-	-
	Stockton	40.28	5068	11	6.20-7.79	7.00	0.14	0.46	6.54
	Mt. Timpanogos	40.24	6000	8	7.00-7.68	7.38	-	-	-
	Provo	40.15	4549	18	6.10-7.62	7.10	0.08	0.36	5.01
	Vineyard	-	-	16	6.20-7.73	7.17	0.10	0.39	5.42
	Provo Canyon	-	5000	12	6.89-7.73	7.25	0.07	0.25	3.48
	Sevier Bridge								
	Reservoir	39.20	5000	11	6.29-7.71	7.04	0.13	0.43	6.07

TABLE 4. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
	Piute Reservoir	38.15	6000	10	6.30-7.43	6.93	0.11	0.34	4.92
	Parowan & Cedar	37.50	5900	17	6.02-7.18	6.79	0.08	0.31	4.59
	Zion N.P.	37.20	4048	6	6.55-7.02	6.78	-	-	-
	Floy	38.56	4000	17	5.75-6.82	6.39	0.08	0.34	5.37
B	Arizona								
	Kayenta	36.44	6300	13	6.90-6.00	6.45	0.08	0.30	4.65
	Prescott	34.34	5280	133	6.00-7.90	7.01	0.03	0.32	4.56
	Phoenix	33.30	1092	11	6.55-7.28	6.85	0.07	0.22	3.21
	Globe	33.23	3541	22	6.50-7.60	7.03	0.06	0.27	3.84
C	Nevada								
	Gerlach &								
	Pyramid Lake	40.40	3900	10	6.40-7.32	6.90	0.11	0.35	5.10
	Reno & Verdi	39.32	4500	10	6.55-7.45	7.07	0.10	0.31	4.40
	Minden	38.58	4600	12	6.58-7.26	6.83	0.06	0.20	2.93
	Hawth. & Walker								
	Lake	38.31	4326	27	6.57-7.95	7.26	0.07	0.36	5.01
	Caliente	37.36	4407	7	6.00-7.21	6.57	-	-	-

TABLE 5. - Data on the variation in width of elytra of male Cicindela oregona.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A,B,C	Alaska								
	Tanana River	63.00	1500	16	2.45-2.81	2.67	0.03	0.11	3.97
A,B,C	British Columbia								
	Terrace	54.31	233	19	2.50-2.90	2.69	0.02	0.10	3.61
	Q. Ch. Islands	53.00	0-4100	7	2.52-2.89	2.75	-	-	-
	Oliver	49.10	2143	36	2.36-3.01	2.67	0.02	0.14	5.17
A	Montana								
	Low.Medicine Lake	48.30	5000	44	2.52-2.93	2.71	0.01	0.10	3.46
	Hardy	47.11	3500	17	2.30-2.83	2.62	0.03	0.14	5.42
	Helena	46.35	4160	28	2.49-2.82	2.65	0.02	0.09	3.25
	Gardiner	45.03	5800	40	2.30-2.90	2.70	0.02	0.12	4.44
A	Wyoming								
	Yellowstone N.P.	44.30	7000	77	2.34-3.10	2.72	0.02	0.14	5.29
	Jackson Hole N.M.	43.50	6800	19	2.40-2.96	2.73	0.03	0.12	4.47
	Moran	43.52	6800	27	2.49-2.85	2.70	0.02	0.11	4.19
	11 miles S.								
	Labarge	42.15	6600	16	2.31-2.86	2.64	0.04	0.15	5.72
	27 miles S.								
	Labarge	42.14	6600	14	2.54-2.75	2.65	0.02	0.07	2.56
	Green River	41.33	6100	30	2.31-2.87	2.62	0.03	0.14	5.46
	Fort Bridger	41.19	6657	38	2.42-2.95	2.71	0.02	0.12	4.46
	Saratoga	41.28	6790	15	2.54-2.80	2.65	0.02	0.07	2.75
	Jelm	41.03	7500	46	2.40-2.88	2.67	0.02	0.10	3.86

TABLE 5. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A	Colorado								
	Estes Park	40.24	7547	12	2.48-2.71	2.62	0.02	0.06	2.29
	Trinidad	37.11	5999	16	2.42-2.69	2.58	0.02	0.07	2.83
A	New Mexico								
	Jemez Springs	35.45	6195	78	2.30-2.79	2.60	0.01	0.10	3.85
	Pecos & Beulah	35.34	7000	10	2.43-2.76	2.60	0.03	0.11	4.23
	Fort Wingate	35.30	6997	13	2.41-2.72	2.56	0.01	0.03	1.17
B,C	Idaho								
	Valley County	45.00	-	7	2.40-2.81	2.64	-	-	-
	Owyhee County	42.30	-	22	2.35-2.81	2.62	0.03	0.13	4.85
	Bear Lake	42.05	5924	61	2.29-2.95	2.66	0.02	0.15	5.60
B	Utah								
	Ogden	41.14	4296	10	2.43-2.95	2.68	0.05	0.16	5.97
	Salt Lake City	40.45	4354	20	2.51-2.98	2.76	0.03	0.12	4.38
	Alta	40.36	8585	2	2.81-2.95	2.88	-	-	-
	Stockton	40.28	5068	11	2.40-2.88	2.70	0.02	0.18	6.81
	Mt. Timpanogos	40.24	6000	8	2.66-2.93	2.83	-	-	-
	Provo	40.15	4549	18	2.50-2.94	2.72	0.03	0.14	5.07
	Vineyard	-	-	16	2.39-2.89	2.70	0.03	0.13	4.96
	Provo Canyon	-	5000	12	2.64-2.95	2.78	0.02	0.09	3.07
	Sevier Bridge								
	Reservoir	39.20	5000	11	2.43-2.92	2.68	0.05	0.15	5.67
	Piute Reservoir	38.15	6000	10	2.50-2.85	2.63	0.04	0.12	4.56

TABLE 5. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
	Parowan & Cedar	37.50	5900	17	2.35-2.80	2.64	0.03	0.11	4.13	
	Zion N.P.	37.20	4048	6	2.50-2.76	2.62	-	-	-	
	Floy	38.56	4000	17	2.20-2.63	2.47	0.03	0.14	5.63	
B	Arizona									
	Kayenta	36.44	6300	13	2.20-2.60	2.44	0.03	0.10	4.10	
	Prescott	34.34	5280	133	2.20-3.00	2.57	0.01	0.12	4.67	
	Phoenix	33.30	1092	11	2.25-2.70	2.53	0.04	0.13	5.14	
	Globe	33.23	3541	22	2.30-2.95	2.56	0.03	0.14	5.47	
C	Nevada									
	Gerlach &									
	Pyramid Lake	40.40	3900	10	2.44-2.77	2.60	0.04	0.13	4.96	
	Reno & Verdi	39.32	4500	10	2.40-2.85	2.65	0.05	0.15	1.51	
	Minden	38.58	4600	12	2.35-2.71	2.56	0.03	0.09	3.16	
	Hawth. & Walker									
	Lake	38.31	4326	27	2.56-3.06	2.77	0.03	0.14	5.02	
	Caliente	37.36	4407	7	2.25-2.74	2.50	-	-	-	

TABLE 6. - Data on the variation in the diameter of the apical dot of male

Cicindela oregona.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
A,B,C Alaska										
	Tanana R.	63.00	1500	16	0.42-0.73	0.59	0.02	0.09	14.51	
A,B,C British Columbia										
	Terrace	54.31	223	19	0.35-0.83	0.63	0.03	0.14	21.75	
	Q. Ch. Islands	53.00	0-4100	7	0.50-0.71	0.62	-	-	-	
	Oliver	49.10	2143	36	0.45-0.83	0.63	0.01	0.08	13.14	
A Montana										
	Low.Medicine Lake	48.30	5000	44	0.34-0.76	0.63	0.01	0.09	14.11	
	Hardy	47.11	3500	17	0.40-0.75	0.55	0.02	0.09	15.73	
	Helena	46.35	4160	28	0.39-0.80	0.65	0.02	0.08	12.91	
	Gardiner	45.03	5800	40	0.43-0.80	0.63	0.01	0.09	14.83	
A Wyoming										
	Yellowstone N.P.	44.30	7000	77	0.28-0.84	0.63	0.01	0.11	16.83	
	Jackson Hole N.M.	43.50	6800	19	0.50-0.73	0.64	0.02	0.08	12.75	
	Moran	43.52	6800	27	0.41-0.90	0.64	0.02	0.10	15.02	
	11 miles S.									
	Labarge	42.15	6600	16	0.52-0.73	0.64	0.02	0.06	9.89	
	27 miles S.									
	Labarge	42.14	6600	14	0.44-0.77	0.63	0.02	0.09	14.60	
	Green River	41.33	6100	30	0.40-0.89	0.64	0.02	0.11	16.72	
	Fort Bridger	41.19	6657	38	0.40-0.83	0.67	0.02	0.09	14.09	
	Saratoga	41.28	6790	15	0.58-0.81	0.68	0.02	0.07	9.63	

TABLE 6. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A	Jelm	41.03	7500	46	0.39-0.85	0.67	0.01	0.10	14.93
	Colorado								
	Estes Park	40.24	7547	12	0.58-0.80	0.69	0.02	0.08	11.45
A	Trinidad	37.11	5999	16	0.61-0.81	0.70	0.02	0.07	9.71
	New Mexico								
	Jemez Springs	35.45	6195	78	0.49-0.85	0.71	0.01	0.08	11.00
B,C	Pecos & Beulah	35.34	7000	10	0.50-0.82	0.67	0.03	0.09	13.43
	Fort Wingate	35.30	6997	13	0.67-0.90	0.78	0.02	0.06	7.69
	Idaho								
B	Valley County	45.00	-	7	0.55-0.78	0.65	-	-	-
	Owyhee County	42.30	-	22	0.45-0.82	0.62	0.02	0.09	14.08
	Bear Lake	42.05	5924	61	0.40-0.78	0.61	0.01	0.09	14.66
B	Utah								
	Ogden	41.14	4296	10	0.50-0.75	0.65	0.03	0.08	12.55
	Salt Lake City	40.45	4354	20	0.44-0.80	0.64	0.02	0.10	15.62
B	Alta	40.36	8585	2	0.65-0.72	0.69	-	-	-
	Stockton	40.28	5068	11	0.62-0.82	0.72	0.02	0.07	9.81
	Mt. Timpanogos	40.24	6000	8	0.57-0.80	0.69	0.08	-	-
B	Provo	40.15	4549	18	0.60-0.81	0.71	0.02	0.06	9.03
	Vineyard	-	-	16	0.50-0.80	0.68	0.02	0.07	10.71
	Provo Canyon	-	5000	12	0.55-0.82	0.69	0.02	0.08	11.57
B	Sevier Bridge								
	Reservoir	39.20	5000	11	0.50-0.82	0.72	0.03	0.08	11.67

TABLE 6. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
	Piute Reservoir	38.15	6000	10	0.55-0.90	0.70	0.04	0.12	16.43	
	Parowan & Cedar	37.50	5900	17	0.55-0.81	0.69	0.02	0.08	11.45	
	Zion N.P.	37.20	4048	6	0.58-0.90	0.76	-	-	-	
	Floy	38.56	4000	17	0.66-0.96	0.79	0.02	0.09	11.84	
B	Arizona									
	Kayenta	36.44	6300	13	0.62-0.90	0.75	0.02	0.08	10.67	
	Prescott	34.34	5280	133	0.55-1.00	0.78	0.01	0.08	10.26	
	Phoenix	33.30	1092	11	0.61-0.88	0.75	0.02	0.08	10.67	
	Globe	33.23	3541	22	0.65-0.90	0.77	0.01	0.07	9.09	
C	Nevada									
	Gerlach &									
	Pyramid Lake	40.40	3900	10	0.62-0.85	0.72	0.02	0.07	10.34	
	Reno & Verdi	39.32	4500	10	0.60-0.81	0.71	0.02	0.07	9.38	
	Minden	38.58	4600	12	0.50-0.75	0.64	0.02	0.09	13.36	
	Hawth. & Walker									
	Lake	38.31	4326	27	0.52-0.90	0.72	0.02	0.09	13.06	
	Caliente	37.36	4407	7	0.55-0.88	0.73	-	-	-	

TABLE 7. - Data on the variation in length of elytra of female Cicindela
oregona.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
A,B,C Alaska										
	Tanana R.	63.00	1500	11	7.65-8.44	7.96	0.08	0.27	3.42	
A,B,C British Columbia										
	Terrace	54.31	223	16	6.56-8.61	7.86	0.12	0.48	6.04	
	Q. Ch. Islands	53.00	0-4100	12	7.48-8.51	8.03	0.10	0.33	4.13	
	Oliver	49.10	2143	24	6.85-8.57	7.79	0.10	0.48	6.21	
A Montana										
	Low.Medicine Lake	48.30	5000	21	6.95-8.25	7.69	0.08	0.37	4.81	
	Hardy	47.11	3500	16	6.56-7.92	7.38	0.09	0.37	5.00	
	Helena	46.35	4160	22	7.04-8.32	7.58	0.07	0.32	4.22	
	Gardiner	45.03	5800	46	6.90-8.55	7.83	0.06	0.39	4.83	
A Wyoming										
	Yellowstone N.P.	44.30	7000	63	7.10-8.49	7.85	0.04	0.34	4.28	
	Jackson Hole N.M.	43.50	6800	8	7.60-8.41	7.91	-	-	-	
	Moran	43.52	6800	19	7.42-8.28	7.82	0.06	0.25	3.17	
	11 miles S.									
	Labarge	42.15	6600	5	7.55-7.91	7.75	-	-	-	
	27 miles S.									
	Labarge	42.14	6600	20	6.72-8.04	7.57	0.09	0.39	5.13	
	Green River	41.33	6100	24	6.88-8.12	7.66	0.07	0.34	4.43	
	Fort Bridger	41.19	6657	26	7.15-8.21	7.66	0.06	0.31	4.07	
	Saratoga	41.28	6790	9	6.46-7.82	7.32	-	-	-	

TABLE 7. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A	Jelm	41.03	7500	42	6.80-8.48	7.57	0.06	0.36	4.73
	Colorado								
	Estes Park	40.24	7547	13	6.98-7.90	7.43	0.08	0.30	3.97
	Trinidad	37.11	5999	10	6.89-7.79	7.23	0.09	0.29	4.05
A	New Mexico								
	Jemez Springs	35.45	6195	85	6.65-8.12	7.47	0.04	0.33	4.42
	Pecos & Beulah	35.34	7000	11	6.83-8.12	7.59	0.11	0.38	5.01
	Fort Wingate	35.30	6997	20	6.50-7.75	7.32	0.07	0.32	4.37
B,C	Idaho								
	Valley County	45.00	-	13	7.00-8.01	7.57	0.09	0.32	4.28
	Owyhee County	42.30	-	40	7.05-8.71	7.80	0.06	0.39	4.97
	Bear Lake	42.05	5924	58	6.45-8.37	7.62	0.06	0.45	5.92
B	Utah								
	Ogden	41.14	4296	3	7.32-7.73	7.59	-	-	-
	Salt Lake City	40.45	4354	21	6.72-8.40	7.71	0.11	0.49	6.41
	Alta	40.36	8585	11	7.34-8.32	7.90	0.09	0.30	3.84
	Stockton	40.28	5068	4	6.71-7.95	7.54	-	-	-
	Mt. Timpanogos	40.24	6000	12	7.40-8.25	7.83	0.07	0.24	3.10
	Provo	40.15	4549	18	6.55-8.55	7.72	0.12	0.51	6.59
	Vineyard	-	-	10	7.08-8.31	7.82	0.12	0.38	4.87
	Provo Canyon	-	5000	14	7.10-8.32	7.83	0.08	0.31	3.96
	Sevier Bridge								
	Reservoir	39.20	5000	10	7.12-7.87	7.52	0.09	0.28	3.71

TABLE 7. -- cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
	Piute Reservoir	38.15	6000	8	6.75-8.00	7.51	-	-	-
	Parowan & Cedar	37.50	5900	13	6.53-8.00	7.49	0.12	0.42	5.61
	Zion N.P.	37.20	4048	20	7.00-8.00	7.44	0.07	0.32	4.26
	Floy	38.56	4000	23	5.96-7.52	6.89	0.09	0.43	6.20
B	Arizona								
	Kayenta	36.44	6300	21	6.25-7.85	6.97	0.07	0.36	5.16
	Prescott	34.34	5280	133	6.70-8.50	7.65	0.03	0.38	4.96
	Phoenix	33.30	1092	15	7.10-8.10	7.54	0.09	0.33	4.38
	Globe	33.23	3541	34	6.62-8.10	7.56	0.07	0.40	5.33
C	Nevada								
	Gerlach &								
	Pyramid Lake	40.40	3900	11	7.32-8.20	7.66	0.10	0.33	4.35
	Reno & Verdi	39.32	4500	10	6.24-8.22	7.58	0.21	0.67	8.84
	Minden	38.58	4600	12	7.57-8.10	7.82	0.05	0.18	2.24
	Hawth. & Walker								
	Lake	38.31	4326	27	6.46-8.60	7.88	0.05	0.49	6.19
	Caliente	37.36	4407	6	6.80-7.72	7.13	-	-	-

TABLE 8. - Data on the variation in width of elytra of female Cicindela
oregona.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
A,B,C	Alaska									
	Tanana R.	63.00	1500	11	2.93-3.20	3.08	0.03	0.08	2.71	
A,B,C	British Columbia									
	Terrace	54.31	223	16	2.50-3.33	3.07	0.05	0.19	6.22	
	Q. Ch. Islands	53.00	0-4100	12	2.85-3.22	3.08	0.03	0.12	3.90	
	Oliver	49.10	2143	24	2.73-3.29	3.07	0.04	0.18	5.93	
A	Montana									
	Low.Medicine Lake	48.30	5000	21	2.59-3.28	3.02	0.04	0.20	6.49	
	Hardy	47.11	3500	16	2.59-3.21	2.93	0.04	0.16	5.43	
	Helena	46.35	4160	22	2.69-3.29	2.98	0.04	0.17	5.57	
	Gardiner	45.03	5800	46	2.69-3.76	3.09	0.03	0.19	6.18	
A	Wyoming									
	Yellowstone N.P.	44.30	7000	63	2.81-3.34	3.10	0.02	0.13	4.32	
	Jackson Hole N.M.	43.50	6800	8	3.03-3.35	3.16	-	-	-	
	Moran	43.52	6800	19	2.85-3.20	3.07	0.02	0.10	3.26	
	11 miles S.									
	Labarge	42.15	6600	5	2.91-3.05	3.02	-	-	-	
	27 miles S.									
	Labarge	42.14	6600	20	2.66-3.10	2.95	0.03	0.13	4.34	
	Green River	41.30	6100	24	2.63-3.25	3.01	0.03	0.15	4.95	
	Fort Bridger	41.19	6657	26	2.72-3.24	3.02	0.02	0.13	4.14	
	Saratoga	41.28	6790	9	2.49-3.05	2.84	-	-	-	

TABLE 8. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A	Jelm	41.03	7500	42	2.70-3.30	3.00	0.02	0.14	4.53
	Colorado								
	Estes Park	40.24	7547	13	2.63-3.17	2.88	0.04	0.15	5.10
A	Trinidad	37.11	5999	10	2.68-3.04	2.86	0.04	0.13	4.51
	New Mexico								
	Jemez Springs	35.45	6195	85	2.60-3.20	2.94	0.01	0.13	4.42
	Pecos & Beulah	35.34	7000	11	2.70-3.24	3.00	0.05	0.15	5.00
B,C	Fort Wingate	35.30	6997	20	2.56-3.17	2.95	0.03	0.13	4.41
	Idaho								
	Valley County	45.00	-	13	2.75-3.20	2.98	0.04	0.15	5.03
	Owyhee County	42.30	-	40	2.68-3.41	3.07	0.02	0.15	4.66
B	Bear Lake	42.05	5924	58	2.52-3.40	3.01	0.02	0.18	5.87
	Utah								
	Ogden	41.14	4296	3	3.00-3.02	3.01	-	-	-
	Salt Lake City	40.45	4354	21	2.78-3.38	3.08	0.04	0.18	5.97
	Alta	40.36	8585	11	2.91-3.30	3.14	0.04	0.12	3.76
	Stockton	40.28	5068	4	2.89-3.20	3.09	-	-	-
	Mt. Timpanogos	40.24	6000	12	2.96-3.25	3.13	0.02	0.08	2.55
	Provo	40.15	4549	18	2.54-3.39	3.07	0.05	0.21	6.91
	Vineyard	-	-	10	2.82-3.32	3.09	0.05	0.16	5.28
	Provo Canyon	-	5000	14	2.86-3.31	3.09	0.04	0.13	4.30
	Sevier Bridge								
	Reservoir	39.20	5000	10	2.80-3.18	2.95	0.03	0.11	3.73

TABLE 8. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
	Piute Reservoir	38.15	6000	8	2.63-3.21	2.95	-	-	-
	Parowan & Cedar	37.50	5900	13	2.79-3.17	3.00	0.03	0.12	3.83
	Zion N.P.	37.20	4048	20	2.85-3.19	3.01	0.02	0.09	3.14
	Floy	38.56	4000	23	2.43-3.05	2.77	0.04	0.17	6.14
B	Arizona								
	Kayenta	36.44	6300	21	2.30-2.90	2.66	0.03	0.16	5.83
	Prescott	34.34	5280	133	2.50-3.30	2.93	0.01	0.16	5.51
	Phoenix	33.30	1092	15	2.60-3.05	2.84	0.04	0.14	4.93
	Globe	33.23	3541	34	2.40-3.20	2.85	0.03	0.18	6.32
C	Nevada								
	Gerlach &								
	Pyramid Lake	40.40	3900	11	2.76-3.33	3.04	0.05	0.16	5.30
	Reno & Verdi	39.32	4500	10	2.45-3.13	2.94	0.07	0.24	8.06
	Minden	38.58	4600	12	2.95-3.16	3.06	0.02	0.08	2.61
	Hawth. & Walker								
	Lake	38.31	4326	27	2.50-3.35	3.10	0.04	0.20	6.39
	Caliente	37.36	4407	6	2.70-2.89	2.82	-	-	-

TABLE 9. - Data on the variation in the diameter of the apical dot of female

Cicindela oregona.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
A,B,C	Alaska									
	Tanana R.	63.00	1500	11	0.58-0.91	0.73	0.03	0.09	12.98	
A,B,C	British Columbia									
	Terrace	54.31	223	16	0.45-0.90	0.72	0.03	0.13	18.33	
	Q. Ch. Islands	53.00	0-4100	12	0.62-0.88	0.76	0.02	0.08	10.50	
	Oliver	49.10	2143	24	0.59-0.91	0.74	0.02	0.09	12.59	
A	Montana									
	Low.Medicine Lake	48.30	5000	21	0.42-0.82	0.68	0.03	0.12	17.21	
	Hardy	47.11	3500	16	0.58-0.80	0.68	0.02	0.07	10.04	
	Helena	46.35	4160	22	0.57-0.90	0.72	0.02	0.10	13.89	
	Gardiner	45.03	5800	46	0.38-0.91	0.74	0.01	0.10	13.70	
A	Wyoming									
	Yellowstone N.P.	44.30	7000	63	0.50-0.92	0.76	0.01	0.10	12.62	
	Jackson Hole N.M.	43.50	6800	8	0.69-0.99	0.81	-	-	-	
	Moran	43.52	6800	19	0.61-0.88	0.75	0.02	0.08	10.43	
	11 miles S.									
	Labarge	42.15	6600	5	0.68-0.85	0.74	-	-	-	
	27 miles S.									
	Labarge	42.14	6600	20	0.54-0.89	0.71	0.02	0.11	14.79	
	Green River	41.33	6100	24	0.51-0.93	0.74	0.02	0.09	12.59	
	Fort Bridger	41.19	6657	26	0.64-1.00	0.80	0.02	0.08	10.60	
	Saratoga	41.28	6790	9	0.63-0.92	0.78	-	-	-	

TABLE 9. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	$\bar{X} \pm$	SE	SD	CV
A	Jelm	41.03	7500	42	0.60-0.94	0.78	0.01	0.07	9.18
	Colorado								
	Estes Park	40.24	7547	13	0.68-0.86	0.77	0.01	0.05	6.49
A	Trinidad	37.11	5999	10	0.70-0.91	0.81	0.02	0.07	8.27
	New Mexico								
	Jemez Springs	35.45	6195	85	0.72-1.05	0.87	0.01	0.08	8.25
	Pecos & Beulah	35.34	7000	11	0.75-1.00	0.88	0.02	0.08	9.09
	Fort Wingate	35.30	6997	20	0.80-1.04	0.92	0.02	0.08	8.70
B,C	Idaho								
	Valley County	45.00	-	13	0.60-0.83	0.72	0.02	0.06	8.00
	Owyhee County	42.30	-	40	0.55-1.00	0.77	0.01	0.09	12.12
	Bear Lake	42.05	5924	58	0.38-1.00	0.74	0.01	0.11	15.41
B	Utah								
	Ogden	41.14	4296	3	0.70-0.80	0.73	-	-	-
	Salt Lake City	40.45	4354	21	0.65-0.96	0.79	0.02	0.08	10.62
	Alta	40.36	8585	11	0.70-1.02	0.80	0.03	0.09	11.19
	Stockton	40.28	5068	4	0.72-0.96	0.88	-	-	-
	Mt. Timpanogos	40.24	6000	12	0.60-0.95	0.83	0.03	0.10	12.53
	Provo	40.15	4549	18	0.70-0.98	0.86	0.02	0.08	9.77
	Vineyard	-	-	10	0.70-0.91	0.81	0.03	0.09	10.90
	Provo Canyon	-	5000	14	0.57-0.89	0.76	0.03	0.10	13.16
	Sevier Bridge								
	Reservoir	39.20	5000	10	0.76-0.95	0.84	0.02	0.06	6.87

TABLE 9. - cont'd.

Rt.	Locality	North lat.	Elev. ft.	N	Range mm	\bar{X}	\pm	SE	SD	CV
	Piute Reservoir	38.15	6000	8	0.70-0.99	0.84	-	-	-	-
	Parowan & Cedar	37.50	5900	13	0.80-0.97	0.86	0.02	0.06	7.50	
	Zion N.P.	37.20	4048	20	0.74-1.00	0.87	0.02	0.07	8.33	
	Floy	38.56	4000	23	0.74-1.05	0.91	0.02	0.08	8.77	
B	Arizona									
	Kayenta	36.44	6300	21	0.75-1.10	0.89	0.02	0.10	11.24	
	Prescott	34.34	5280	133	0.75-1.20	0.93	0.01	0.09	9.68	
	Phoenix	33.30	1092	15	0.75-1.05	0.90	0.02	0.08	8.89	
	Globe	33.23	3541	34	0.65-1.05	0.90	0.01	0.08	8.89	
C	Nevada									
	Gerlach &									
	Pyramid Lake	40.40	3900	11	0.60-0.94	0.78	0.03	0.09	11.47	
	Reno & Verdi	39.32	4500	10	0.65-0.87	0.79	0.02	0.07	9.48	
	Minden	38.58	4600	12	0.61-0.98	0.79	0.03	0.10	12.03	
	Hawth. & Walker									
	Lake	38.31	4326	27	0.60-1.00	0.84	0.02	0.10	11.67	
	Caliente	37.36	44.07	6	0.70-0.92	0.81	-	-	-	

4.43 Cicindela depressula Casey

Cicindela depressula depressula Casey 1897:297. Type locality--Placer County, California. Leng 1902:150. Rivalier 1954:253.

Cicindela oregona depressula Hatch (not Casey 1897) 1953:42.

Horn 1930:82. Wallis 1961:24.

Cicindela depressula eureka Fall 1901. Type locality--Humboldt County, California. NEW COMBINATION.

Cicindela eureka Fall 1901:307. Leng 1902:149. Horn 1930:82.

Rivalier 1954:253.

Two constant differences set apart depressula from other species of the maritima group. First, in depressula two or three hairs usually occupy the small area near the front inner edge of each eye; four hairs are seldom present. If these hairs are abraded, setigerous punctures indicate their former positions. Second, the distal end of the median lobe of the male genitalia of depressula has two distinct, broad flanges that form a blunt apex (for details see Fig. 3, and Sec. 3.2). A partially diagnostic character is the form of the middle band of the elytra. In Oregon and California the middle band of depressula tapers evenly posteriorly. This contrasts with the sharp bend in the middle band of oregona. On the other hand in Washington, Canada, and Alaska the middle band of depressula often appears identical with that of oregona.

I collected oregona and depressula eureka on the same sand bank along the Van Duzen River near Bridgeville, California; and Ball (personal communication) collected d. depressula and o. guttifera in the same area at Terrace, British Columbia, and at Haines, Alaska. There was no evidence of

hybridization or cross-mating at these locations, and this suggests that depressula and oregona are specifically distinct in spite of their many shared characteristics.

Notes on synonymy

The tiger beetles called depressula and eureka are very similar to one another, differing mainly in color and markings of the elytra and in seasonal occurrence of adults. They are also allopatric. The differences, however, are not absolute; that is, range of variation in the diagnostic characters of the two forms is slightly overlapping. Furthermore, Rumpp has from the Olympic National Forest, Washington, a series of specimens interpreted as hybrids between depressula and eureka. These considerations of variation and distribution suggest that depressula and eureka are conspecific, but are subspecifically distinct. Rumpp and I have reached this conclusion independently.

Geographic variation and subspecies

Eleven population samples, whose geographic positions collectively span the known range of this species were selected on the basis of geographical location and number of specimens and were examined for variation. Elytral size, elytral color, pleural color, presence of humeral dot on elytra, and the condition of the middle band vary. Variation in these was analysed and the results are summarized in Tables 10 - 14.

Length of elytra.- This was examined in a cursory fashion (Table 10). Mean values for females are higher than those for males of the same locality. Mean values for samples from lowland, coastal regions in

Humbolt County, California are normally higher than mean values for populations from Mount Rainier, Washington. This is the reverse of the pattern of size variation in oregona.

Phenology.- Populations of the Cascade Range differ in phenology from those of the Pacific coast of Oregon and California. At these latitudes populations from these regions do not meet, for apparently there is a difference in seasonal occurrence of adults. Most adults in alpine regions are active during the middle and late summer but in coastal populations the adults are out earlier in the year. On a collecting trip in June 1963 depressula was not found at high elevations, but specimens of coastal populations were collected in northwestern California.

Color of elytra.- Elytra of depressula have a metallic lustre and are either brown, green or blue (Table 11). There is no evidence of a uniform character gradient. Brown elytra are prevalent in coastal regions of northern California, on Mount Hood, Oregon and on Mount Rainier, Washington. Specimens with green elytra occur throughout the range of the species, but are most frequent at both northern and southern extremities of the range, e.g. Haines, Alaska and Eldorado County, California. Blue elytra are most common in populations from Washington and southern British Columbia and as such parallel those of oregona in southwestern British Columbia. In California, over 90 per cent of specimens from Cascade Range localities are green, whereas over 90 per cent from the coast are brown.

Color of thoracic pleura.- Except for Lassen National Park and Eldorado County, California, this feature is rather variable in every population listed in Table 12. Specimens with green and coppery thoracic

pleura are more common than those with blue.

Humeral dot.- Data on variation in this characteristic are presented in Table 13. The humeral dot is present in all specimens collected in lowland localities near the Pacific coast. Among specimens from localities in the Cascade Mountains, the dot may be present or absent. Over 90 per cent of the specimens from north of and including Mount Baker, Washington have humeral dots on the elytra, but only 10 per cent of the specimens from southern Oregon and California have them. In the Mount Rainier, Washington and Mount Hood, Oregon samples the two conditions occur in about equal frequencies. The variation appears to be clinal.

Middle band.- The middle band of the elytra may be broken or complete, and the data on the frequencies of these conditions in various population samples are presented in Table 14. In general the broken condition of the middle band is more common southward, among montane populations, but this is a poorly marked trend. All of the specimens from coastal regions in California have a complete middle band.

Hair between eyes.- Variation in this character is not tabulated. However, between the eyes, in the middle of the head, one to four very fine hairs are present in coastal specimens from southern localities. The hairs rarely appear on specimens from northern montane regions, or on specimens from montane localities in California. These hairs should not be mistaken for the setae near the front inner edge of the eyes that are characteristic of depressula as a whole.

Discussion.- Most northern populations studied exhibit appreciable

variation. The five specimens from Haines, Alaska are less variable but more material is necessary from northern localities to obtain a better knowledge of the degree of variation. In the central portions of the range, variation is discordant. Southern populations, however, are remarkably uniform.

Of the characters considered above, specimens collected in southern areas of the Cascade Range vary mainly in the condition of the middle band. Almost all of these specimens have the elytra and thoracic pleura green, and no humeral dot. These characters are generally most common in northern populations.

Mountain populations of California and Oregon are distributed in a thin band along the Cascade Range where they are confined to high altitudes, but further north they also occur in the Rockies (Mount Revelstoke, British Columbia) and altitudinal preference is not as marked as in southern regions (Fig. 33).

Coastal specimens from California differ in external characteristics from alpine individuals at the same latitude. Specimens from these lowland regions usually have brown elytra, a very long, usually complete middle band, a humeral dot, and coppery, green or blue thoracic pleura. They occupy river banks near the Pacific coast of northern California, Oregon and Washington. Few specimens of this type have been collected in Oregon and Washington. They may not be abundant in these regions; or perhaps the adults come out only for a short period. On the other hand, more intense collecting in May and June may yield larger numbers of these forms from coastal areas of Oregon and Washington.

These differences provide the basis for distinguishing two subspecies: a southern coastal one d. eureka Fall and a mountain northern one, d. depressula Casey.

Variation in some morphological characters, phenology, hybridization, and distribution of depressula and eureka have been discussed above. However the apparently restricted distribution of eureka should be discussed further.

Distribution limits of eureka north of California are poorly understood because material is very scanty. In June 1963, a collecting expedition to the American southwest was carried out in order to obtain specimens of depressula and oregona. While in Humbolt County, California we obtained several large series of eureka near the mouths of Redwood Creek, and Mad and Van Duzen Rivers. Travelling from west to east in the Van Duzen River valley, we collected eureka as far east as Bridgeville which is approximately 1,000 feet above sea level and 30 miles east of the Pacific coast. Fifteen miles east of Bridgeville at an elevation of about 2,000 feet eureka was not present, nor was eureka present along Redwood Creek, 17 miles east of the Pacific coast. Thus the eastern limit of eureka is a short distance from the coast. At this latitude average temperature differences due to altitude may play a part in limiting eureka so closely to the coast. However much ecological information is essential in order to understand the forces which confine eureka to such a restricted region in California.

Subspeciation.- C. depressula evolved in western North America probably as a cool-adapted lowland species, having shared a common ancestry

with duodecimguttata. During a fairly recent glacial stage the range of the species was bisected by mountain glaciers with survivors to the west and to the east of the Cascades at low elevations. During this period of isolation differentiation occurred, with the coastal populations evolving the least in color pattern, but becoming bound to climatic conditions existing at lower elevations. This group became the subspecies eureka. As the glaciers retreated and the inland refugium became warmer and drier the populations isolated there (d. depressula) moved up the mountains and/or northward. Differentiation then occurred in d. depressula with the southern members developing a reduced amount of white markings. In northern Washington the ranges of the two isolates met and hybridization took place.

Distribution patterns like that of depressula are evident in vertebrates such as Sorex vagrans Baird (Findley 1955), Rana aurora, Baird and Girard, and Contia tenuis Baird and Girard (Stebbins 1954).

Distribution

Of the 922 specimens of depressula examined, one appears to be incorrectly labelled. This specimen is labelled Berkeley, Alameda County, California, but it was probably not collected in this locality. The specimen does not resemble the subspecies d. eureka but it is phenotypically d. depressula the distribution of which is restricted to the Cascade Range at that latitude.

C. depressula depressula Casey. Canada. BRITISH COLUMBIA:
Diamond Head Trail, Garibaldi Park, 14; Jade Lake Trail, Mount Revelstoke, 1;
Terrace, 4.

United States. ALASKA: Haines Highway, near Haines, 5.

CALIFORNIA: Alpine County: 7. Eldorado County: Echo Lake, 15; Fallen Leaf Lake, 2; Keith Dome, 11; Mount Tallac, 10; Summit, 3. Mariposa County: Kerrick Meadows, Yosemite National Park, 2. Nevada County: Rucker Lake, 1. Placer County: Summit, 2. Shasta County: Kings Creek, Lassen Park, 6; Mount Lassen, 18. Siskiyou County: Walker, 3. Localities of unknown counties: Angora Park, 3; Carson Pass, 2; Charity Valley, 1; Sovoft, Sierra Nevada Mountains, 1; Warner Valley, 2. NEVADA: Washoe County: Mount Rose, 2. OREGON: Deschutes County: Three Creeks, 1; Todd Lake Meadows, 1. Douglas County: Diamond Lake, 1; Three Lakes, 1. Hood River County: Mount Hood, 54. Jackson County: Mount Ashland, 2. Jefferson County: Mount Jefferson, 1. Josephine County: Rogue Riffles, 1. Klamath County: Crater Lake, 60; Summit Lake, 2. Lake County: Linton Meadows, near Three Sisters area, 17. Lane County: Obsidian Trail, 1; Scott Lake, 9; Wikiup Plains, 5. Linn County: Big Lake, 1; Hoodoo, 2; Santiam, 1. Yamhill County: McMannville, 1. WASHINGTON: Clallam County: Forks, 6. Clark County: Vancouver, 4. Cowlitz County: Silverlake, 2. King County: Enumclaw, 1; Red Mountain, 1. Kittitas County: Cle Elum, 1. Pierce County: 1; Long Mire, 3; Mount Rainier, 461. San Juan Islands, 1. Skamania County: Little Huckleberry Mountain, 1. Snohomish County: Arlington, 3; Soda Springs, 1; Sultan, 1. Whatcom County: Mount Baker, 9. Yakima County: Naches Pass, 4. Localities of unknown counties: Chinook Pass, 8; Greenwater, 2; Lake Cushman, 3; Mora, 2; Mount Adams, 13; Pilchuck Mountain, 1; Stillguamish, 2; Verlot, 1.

C. depressula eureka Fall. United States. CALIFORNIA: Humbolt County: Alton, 2; Arcata, Mad River, 39; Blue Lake, 4; Bridgeville near

Van Duzen River, 19; Fortuna, 1; Orick, Redwood Creek, 12; Scotia, 1;

Van Duzen River, 27. Del Norte County: Requa, 3; Terwah, 1. OREGON:

Benton County: Corvallis, 1. Linn County: Albany, 1. WASHINGTON:

King County: Seattle, 1. Whatcom County: Naches Pass, 1.

TABLE 10. - Data on variation in length of elytra of male and female
d. depressula and d. eureka.

	Sex	N	Range mm	\bar{X}	\pm SE	SD	CV
<u>d. depressula</u>	male	25	6.62 - 8.07	7.25	0.07	0.35	4.83
<u>d. depressula</u>	female	25	6.70 - 8.42	7.60	0.08	0.38	5.00
<u>d. eureka</u>	male	25	6.72 - 8.12	7.51	0.06	0.32	4.21
<u>d. eureka</u>	female	25	7.35 - 9.03	8.31	0.08	0.42	5.02

TABLE 11. - Data on color variation of elytra of population samples
of Cicindela depressula.

<u>d. depressula</u>	Color of elytra					
	Brown		Green		Blue	
	N	%	N	%	N	%
Haines, Alaska	1	20	4	80	0	0
Garibaldi Park, B.C.	1	6	7	47	7	47
Mount Baker, Wash.	1	8	5	42	6	50
Mount Rainier, Wash.	201	45	115	25	135	30
Mount Hood, Oregon	40	89	5	11	0	0
Crater Lake, Oregon	8	14	45	76	6	10
Lassen Nat. P., Calif.	0	0	22	96	1	4
Eldorado County, Calif.	0	0	25	96	1	4
<u>d. eureka</u>						
Orick, Red. Ck., Calif.	12	100	0	0	0	0
Arcata, Mad River, Calif.	38	100	0	0	0	0
Van Duzen River, Calif.	41	89	5	10	0	0

TABLE 12. - Data on color variation of thoracic pleura among population samples of Cicindela depressula.

Color of Pleural Sclerites						
<u>d. depressula</u>	Copper		Green		Blue	
	N	%	N	%	N	%
Haines, Alaska	4	80	1	20	0	0
Garibaldi Park, B.C.	8	53	6	40	1	7
Mount Baker, Wash.	2	17	6	50	4	33
Mount Rainier, Wash.	200	44	208	46	43	10
Mount Hood, Oregon	33	73	12	27	0	0
Crater Lake, Oregon	9	15	44	75	6	10
Lassen Nat. P., Calif.	1	4	21	92	1	4
Eldorado County, Calif.	1	4	24	92	1	4
<u>d. eureka</u>						
Orick, Red. Ck., Calif.	3	25	5	42	4	33
Arcata, Mad River, Calif.	3	25	5	42	4	33
Van Duzen River, Calif.	5	11	31	67	10	22

TABLE 13. - Data on the occurrence of elytral humeral dot among
population samples of Cicindela depressula.

<u>d. depressula</u>	N	Specimens with dot/N	%
Haines, Alaska	5	5/5	100
Garibaldi Park, B.C.	15	14/15	93
Mount Baker, Wash.	12	11/12	92
Mount Rainier, Wash.	451	232/451	51
Mount Hood, Oregon	45	26/45	58
Crater Lake, Oregon	59	1/59	2
Lassen Park, Calif.	23	0/23	0
Eldorado County, Calif.	26	0/26	0

d. eureka

Orick, Red. Creek, Calif.	12	12/12	100
Arcata, Mad River, Calif.	38	38/38	100
Van Duzen River, Calif.	46	46/46	100

TABLE 14. - Data on variation in the condition of the middle band of elytra among population samples of Cicindela depressula.

<u>d. depressula</u>	N	Specimens with complete band/N	%
Haines, Alaska	5	4/5	80
Garibaldi Park, B.C.	15	13/15	87
Mount Baker, Wash.	12	12/12	100
Mount Rainier, Wash.	451	429/451	95
Mount Hood, Oregon	45	29/45	65
Crater Lake, Oregon	59	9/59	15
Lassen Park, Calif.	23	13/23	57
Eldorado County, Calif.	26	19/26	73

d. eureka

Orick, Red. Creek, Calif.	12	12/12	100
Arcata, Mad River, Calif.	38	38/38	100
Van Duzen River, Calif.	46	46/46	100

5.0 HYBRIDIZATION BETWEEN C. OREGONA AND C. DUODECIMGUTTATA

5.1 Introduction

Cicindela duodecimguttata ranges across most of eastern and central North America from Texas to northern Canada, and from the eastern slopes of the Rocky Mountains to the Atlantic (Fig. 17). Cicindela oregona occupies regions in and west of the Rocky Mountains to the Pacific coast from southern United States to Alaska (Fig. 18).

During the glacial stages of the Pleistocene the two forms were probably isolated from one another, oregona to the west of the Rockies and duodecimguttata to the east of that mountain range. Since Pleistocene times their ranges have expanded and have come together forming a zone of intergradation on the eastern slopes of the Rocky Mountains, that extends from Colorado to northwestern Canada. This hybrid zone is approximately 50 miles wide in the North Saskatchewan River valley in western Alberta, but it is nearly 1,000 miles wide in northwestern Canada. As far as is known hybridization between these two species occurs in all areas of sympatry. The objectives of this section are to indicate the extent of hybridization in these tiger beetles, temporal variation in several hybrid populations, and to provide information on other facets of their interbreeding.

This study is based on 19 population samples comprising 1,731 adult specimens of which 1,291 were collected in Alberta, 205 in the Northwest Territories, 75 in British Columbia, 70 in Montana, 61 in Saskatchewan, 27 in Alaska and 3 in Colorado (see Fig. 34). Additional material from areas east and west of the hybrid zone was obtained from

various North American institutions and has been analysed in the oregona and duodecinguttata taxonomic sections of this thesis. (4.41, 4.42).

Adult male and female duodecinguttata are alike in color, color pattern, and distribution of hair on the head. Hairs cover the frons, top of the head, and post genae. In the western portions of the range of this species individuals are brown dorsally and metallic blue-green ventrally, the prothoracic pleura are coppery, and they have complete elytral patterns (for details see Sec. 4.41).

The species duodecinguttata hybridizes with the subspecies oregona guttifera. Both sexes of this subspecies have similar external features. Hairs are not present on the post genae, frons or top of the head, but a few occupy a small area near the front inner edges of the eyes. The color is identical to that of duodecinguttata - brown dorsally and blue-green ventrally, and coppery prothoracic pleura. A reduced elytral pattern is characteristic of oregona with humeral and apical lunules each represented by two dots, and the marginal band absent.

Elytral pattern, and distribution of hair on the head were used to develop a hybrid index for duodecinguttata and oregona. Male genitalia were not used because it seemed preferable to use characteristics occurring in both sexes. High values were assigned to the characteristics of duodecinguttata. Conversely low values were ascribed to the characteristics of oregona. Intermediate expressions of these characteristics were scored with intermediate values. These characteristics are illustrated in Figs. 11 to 16 and details of assignment of values are given in Table 15. In population samples of non-hybrid duodecinguttata from western localities,

index values range from 4 to 7; and in non-hybrid populations of oregona, values range from 0 to 1.

Characteristics of oregona and duodecimguttata occur in many recombinations in the hybrids. Many specimens are like one of the parental types except for one character while others have index values of 2 or 3. Specimens that have hairs on the frons and head often have hairy post genae. This could be a pleiotropic effect of a single gene, but since the association is inconstant the post genae and frons are treated as separate characters.

5.2 Variation in space

A hybrid index value was determined for each of the 1,731 specimens. A histogram shows the percentage of specimens per index value for each population sample (Figs. 35 - 43). The localities from which populations samples were collected are illustrated in Fig. 34 except localities that are represented by only a few specimens.

The samples are arranged in four groups for purposes of discussion; a transect from Vancouver, British Columbia to Saskatoon, Saskatchewan, via the Saskatchewan River system; the Belt Creek, Montana sample; the Boulder, Colorado sample; and a transect from Tanana River, Alaska to Fort Smith, Northwest Territories through Norman Wells, Northwest Territories.

5.21 Vancouver - Saskatchewan River drainage transect

Three portions of the transect serve to illustrate spatial phenotypic changes between uncontaminated populations of oregona and uncontaminated duodecimguttata through a zone of intergradation centred

in the upper regions of the North Saskatchewan River valley. The transect lies on a west-east plane with the geographically extreme points Vancouver in the west and Saskatoon in the east. The first part includes population samples from Vancouver and Creston. The second portion of the transect is along the western regions of the North Saskatchewan River valley and includes population samples from Kootenay Plains, Nordegg, Saunders, Rocky Mountain House, and Lodgepole. The Edmonton and Saskatoon samples constitute the eastern portion of the transect. Air mile distances and index changes per mile between localities are also given in the figure. Histograms illustrating variation in population samples from Lethbridge, Saskatchewan Crossing, Garth, Crimson Lake, and eight miles south of Lodgepole provide additional data.

a. General trend (Fig. 35)

Vancouver.- These specimens were collected in Vancouver, British Columbia on a sand bank bordering an inlet of the Pacific Ocean. All the individuals score 0 indicating a pure oregona population.

Creston.- This locality is 285 air miles east of Vancouver. The sample is composed of 48 specimens of which 21 were taken by Stace-Smith in 1945 and 27 by Ball in 1957. Only one specimen scores 1, while the remaining score 0. Average index change per mile, from Vancouver to Creston is 0.0001 which is negligible and can be attributed to natural variation in the Creston population.

Kootenay Plains.- In 1962 specimens were collected near the Kootenay Plains, 20 miles down stream from the junction of the Banff-Jasper highway and the North Saskatchewan River. River banks are steep near the

Plains and are covered with undergrowth to the edge. These banks are therefore not suitable for riparian tiger beetles such as oregona. However, many islands formed by sand and clay deposits occupy the river bed and divide the river into several large streams. Most of these islands are sparsely covered with grass and shrubs, and river debris such as drift wood is plentiful. The islands proved to be suitable habitat for oregona and another riparian species, C. repanda. One specimen scores 1 and represents 7.15 per cent of the population sample. All other individuals score 0. The average index value for the sample is 0.07.

Nordegg.- Sand and mud islands that characterize the North Saskatchewan River near Kootenay Plains are also present 24 miles downstream at the Forestry Trunk Road crossing near Nordegg. Two islands divide the river into three large streams. Three road bridges link the islands with one another and the river banks. The southern island bears large shrubs which occupy higher central portions, while grass is abundant throughout. Much of the west half of the island is a clay flat that is periodically covered with water when the river rises. The soil there is basic with a pH of 8.2. Within the soil, organic matter is virtually absent but free lime is very high. Riparian tiger beetles are abundant on the island especially along the clay flat. A series of 174 specimens was collected in 1963; the population sample is variable, composed of oregona, duodecimguttata, and hybrid individuals. The index values range from 0 to 7, with the average at 0.74. Since all indices but 5 are represented the population is more variable than morphologically extreme populations of either of the parental species. Of the population sample 76 per cent score 0, four per cent score 7, and 26 per cent have intermediate values. The

average index value increases 0.03 units per air mile from Kootenay Plains to Nordegg, which is 300 times greater than that from Vancouver to Creston.

Saunders.- Fifteen air miles east of Nordegg the North Saskatchewan River is narrow and no islands are present. The north shore is a sandy strip several to 10 feet wide and littered with drift wood. The river banks descend sharply to the sandy shore line, and are covered with undergrowth for the most part but grassy clearings are present. These clearings are probably periodically inhabited by riparian tiger beetles when the river is high and covers the sandy shore margins. C. oregona, duocecinguttata and hybrid individuals are abundant on the beach at Saunders from which a series consisting of 64 specimens was taken in 1963.

The range in index values is 0 to 7 with the average at 2.31. This is a mean index increase of 0.11 per mile from Nordegg to Saunders, that is, more than three times the average index increase per mile from Kootenay Plains to Nordegg. Specimens with an index of 0 comprise 43.8 per cent of the population sample, while those which score 7 constitute 15.6 per cent. Individuals which score 2 to 6 inclusive make up 40.6 per cent of the sample. No specimen received an index value of 1.

Rocky Mountain House.- Thirty-four miles east of Saunders, at the Highway 11 bridge near Rocky Mountain House, the river banks are flatter and broader than those upstream. A mixture of clay, sand and loose gravel forms the south bank near the bridge. Open patches are common on which tiger beetles are active.

The index values range from 0 to 7 and the average is 6.14. Specimens scoring 7 comprise 64.7 per cent of the population sample while individuals with

a value of 0 constitute 1.5 per cent. Most hybrids resemble duodecimguttata more closely than oregona. Although non-hybrid oregona is scarce in this predominantly duodecimguttata population many hybrid individuals are present.

Brazeau River, ten miles south of Lodgepole.- Large sand banks flank the north side of the river adjacent to the Brazeau power house. Because a dam has been erected further upstream, only a little water is present near the power house and much of the river bed is exposed. On August 12, 1963 a population sample was collected on the sand banks near the Brazeau power house.

The specimens have index values that range from 0 to 7 but none score 4 or 6. The average index is 2.29. Because the Brazeau power house is located near the North Saskatchewan River between Rocky Mountain House and Edmonton, it would appear that the mean index value of a population sample from that area should fall between 6.14 and 6.77, the average indices of Rocky Mountain House and Edmonton respectively. In fact, the average index is approximately 4 less than expected. This may be in part because the Brazeau power house locality although downstream from Rocky Mountain House is 17 miles west of it. In addition, oregona and duodecimguttata exhibit different habitat preferences (see locality eight miles south of Lodgepole). The pure sand bank near the power house is particularly suitable for oregona and thus harbors a population with a lower average index value than that at Rocky Mountain House.

Edmonton.- This sample was collected in 1961 near the Groat Bridge within the city limits. The average index value is 6.77 and the

range is 4 to 7 inclusive. This may be the result of hybridization with oregona but is more likely natural variation.

Saskatoon.- This sample was collected in 1962. The mean index value is 6.76 which is a change of 0.00003 index units per mile from Edmonton to Saskatoon a distance of 310 air miles. A small percentage of the Saskatoon sample with values of 2 and 3 is interpreted as natural variation in a non-hybrid duodecimguttata population. It is the result of breakdown of the elytral markings, which is probably caused by duodecimguttata genes infiltrating from the east, rather than oregona genes from the west.

b. Additional localities in western Alberta

Saskatchewan Crossing (Fig. 36).- These specimens were collected near the junction of the North Saskatchewan River and Banff-Jasper Highway about 20 miles west of the Kootenay Plains. All the individuals score 0.

Garth (Fig. 37).- This locality is approximately three miles upstream from Rocky Mountain House. The river on the north side is a clear stretch of sand and clay. In May, 1963 a sample was taken on this beach.

The index values range from 0 to 7. Most specimens score high and the average index is 5.25. If this is compared with the histogram for the Rocky Mountain House sample (Fig. 38), that was collected on the same day, the mean index difference is 1.24.

Crimson Lake (Fig. 39).- Crimson Lake is about nine miles north

of Rocky Mountain House. At the east end the water front is sandy. For about 500 feet and at the south end of this beach the sand is light in color and loose and C. repanda is abundant. Toward the west end of the beach the ground is a hard and dark mixture of sand and clay and is flanked by a marshy area. Many duodecinguttata individuals were active in this area of the beach and repanda was absent.

Samples were collected at Crimson Lake in 1961, 1962 and 1963. The range of average index values is 6.14 to 6.55. Several oregona specimens were collected here, but they are rare. The population is mainly duodecinguttata with evidence of oregona gene infiltration.

Eight miles south of Lodgepole (Fig. 40).- Many ponds are scattered beside the gravel highway between Lodgepole and the Brazeau power house. These are water-filled gravel pits that were dug out for road construction. The soil around the ponds is normally hardened clay covered with grass. The same day the Brazeau River power house specimens were taken, I also collected 17 specimens near one of these roadside ponds, two miles north of the Brazeau power house.

The hybrid index values of the roadside samples range from 3 to 7, and the average index is 6.36. This index average is 4.07 more than the mean index of the Brazeau power house population.

The marked average index difference between populations of the Brazeau power house and roadside ponds is indicative of different habitat preferences of the two species. Populations of oregona are best adapted to pure sand and clean gravel, commonly found along mountain streams. The species duodecinguttata normally inhabits edges of lakes, sloughs, and rivers

where there are usually flat clearings of dark sand, clay or mud. Wherever these two habitats are available together, at least near the North Saskatchewan River, duodecimguttata and oregona hybridize. Because the soils around the roadside ponds between Lodgepole and Brazeau power house are predominantly clay, they were probably first inhabited by duodecimguttata individuals which invaded these ponds from sloughs etc. nearby. However, the effect of oregona is evident in these roadside populations.

Lethbridge.- The Lethbridge sample consists of 310 specimens that were collected throughout the summer of 1962 (Fig. 41). More than 84 per cent of the specimens are pure duodecimguttata. No individuals score 0 or 1. The index range is 2 to 7 inclusive with the average at 6.7. The histogram indicates that some introgression from oregona is influencing this predominantly duodecimguttata population.

In 1960 two oregona specimens were collected near Lethbridge. The occurrence of these specimens supports the supposition that variation in Lethbridge is the result of hybridization between oregona and duodecimguttata.

Histograms are not provided for the following population samples.

High River.- This locality is 30 miles south of Calgary. Of the four representative specimens there are two hybrids, one oregona, and one duodecimguttata.

Happy Valley.- In 1925 F.S. Carr collected eleven specimens from this locality, which is near the Bow River approximately four miles west of Calgary. The sample consists of six oregona, two duodecimguttata and three hybrids.

Ricinus.- These specimens were taken in 1961 by Wu near the Clearwater River, 20 miles south of Rocky Mountain House. Two individuals are duodecimguttata and one is a hybrid.

Beaver Creek.- The locality and collector of this small sample are both unknown. Two specimens are duodecimguttata and one is a hybrid.

5.22 Belt Creek, Montana (Fig. 42)

In 1963 a sample was collected along Belt Creek just east of Arlington, Montana. Specimens of both oregona and duodecimguttata were taken with hybrids.

All of the index values are represented, but oregona specimens represent 64.3 per cent of the sample while two individuals score 7 and constitute 2.9 per cent of the series. The index mean is 1.23.

There are mean differences in index values between males and females. Values for males do not exceed 5, and the mean index value is 0.70. Thirty-four females show a range in values from 0 to 7 and their average index is 1.79; that is, 1.09 more than the males which total 36. In other samples, the differences between males and females is less.

5.23 Boulder, Colorado

The southernmost hybrid sample is represented by two duodecimguttata specimens and one hybrid which were collected four miles north of Boulder, Colorado in July 1960. A histogram is not provided for this sample.

5.24 The Alaska - Fort Smith transect

This transect, composed of population samples collected at the Tanana River, Alaska, Norman Wells, Northwest Territories, and Fort Smith, Northwest Territories extends over a range of about 1,000 miles (Fig. 34). Index values were determined for all of the specimens and a histogram is presented for each of the three samples (Fig. 43). Included in the figure are air mile distances and index changes per mile between the localities.

Tanana River.- In 1958 Ball collected a series of specimens at a junction of the Tanana River and the Alaska Highway in southeastern Alaska. Specimens that have an index value of 0 constitute 88.9 per cent of the sample, while two individuals, representing 11.1 per cent each score 1, because both have hairs on their heads. The average index value is 0.11.

Norman Wells.- This locality, situated near the MacKenzie River, is approximately 470 miles east-northeast of the Tanana River locality. Index values range from 0 to 7 with the average at 2.68. The average index change per mile from Tanana River to Norman Wells is 0.00547. The sample exhibits a great amount of variation and hybrids outnumber the parental forms. One specimen scores 0 and two members each have values of 7. Thus the parental specimens together constitute only 6.9 per cent of the sample. In contrast individuals that score 2 occur in the greatest frequency and make up 69.9 per cent of the sample. It has been pointed out earlier that natural variation in an uncontaminated duodecimguttata sample may include specimens indexed from 2 to 7. Similarly a pure oregona population can have individuals that score 1 as well as 0. Thus a true hybrid is considered to have a value of 2 or 3. Because specimens with scores of 2 and 3 dominate the Norman Wells sample it is regarded as a predominantly hybrid population sample and

is the only one of its kind in this study.

Fort Smith.- These specimens were collected near the Slave River, 580 miles southeast of Norman Wells. Index values range from 2 to 7 with the average at 5.97. From Norman Wells to Fort Smith the change per mile is 0.00567 units. No specimens have values of 0 or 1. Individuals that score 2 occur in lowest frequency while those with a value of 7 are most numerous. The number of specimens increases with increasing index values. The sample is therefore a duodecimguttata one affected by introgression of oregona characteristics.

Histograms are not provided for the two following localities.

Canol.- Of the five specimens taken near the McKenzie River opposite Norman Wells there are one oregona, one duodecimguttata and three hybrids.

Fort Simpson.- One oregona specimen and one hybrid were taken at this locality which is 290 miles southeast of Norman Wells near the mouth of the Liard River.

5.3 Variation in time

Annual and seasonal variation in index values appear to be typical of most localities in the western section of the North Saskatchewan River. Variation is illustrated by histograms for population samples collected in the Nordegg area, near Rocky Mountain House, at Crimson Lake, and in an area eight miles south of Lodgepole.

5.31 Nordegg (Fig. 44)

Evidence of extensive hybridization is clearly shown in the histogram for the 1961 sample. Index values range from 0 to 7 and the average is 2.60. Specimens of oregona are most common, constituting 39.8 per cent of the sample. Specimens of duodecimguttata follow in number and are 25.3 per cent of the sample. The remaining portion of the series is formed by intermediate specimens which are mainly at the low end of the index scale.

The situation is markedly changed in 1962. A shift toward the low end of the histogram occurs. Specimens that score 0 increase to 74.2 per cent, while specimens with an index of 7 drop to 6.8 per cent of the sample. The average index is 0.97, a drop of 1.63 from the previous year. There is a further depletion in duodecimguttata numbers in 1963 but there is very little general change in the frequency of indices from that of 1962.

This may be a phase in fluctuating populations of the parental forms. However many more years of sampling at Nordegg would provide a clearer picture of annual variation in these populations. Analysis of Nordegg population samples collected in May, July, and August, 1963, revealed a slight trend in decrease of average index values throughout the summer.

Values for the May sample, range from 0 to 7, excepting 4, 5, and 6, with the average at 0.98. The sample is therefore predominantly oregona specimens (71 per cent), some hybrids closely resembling oregona, and five phenotypic duodecimguttata individuals. In the July sample more classes are present, and only index value 5 is not represented. The index

value is 0.72, which is 0.26 less than that of May. Specimens with high index values are all but absent in the August sample. Only two individuals with values of 6 and 7 comprise 3.40 per cent of the population sample. All other specimens are at the low end of the scale with the largest number at 0.

There also appears to be a seasonal change in the relative numbers of males and females at Nordegg. The ratio of males to females in the May population sample is approximately 1 to 1 (27 males and 35 females), but males outnumber females in the July sample, 2 to 1 (36 males and 18 females). In the August series, the ratio of males to females is approximately 3.7 to 1 (45 males and 13 females). Females are most abundant in May and decrease in number throughout the summer.

5.32 Rocky Mountain House (Fig. 38)

The range in index values for the May series is 3 to 7 with the average at 6.49. Of the sample, 24 specimens score 7. Thus the population sample is basically a duocecinguttata one somewhat contaminated by oregona genes.

The August sample is more variable and all the index values except 2, are represented. The average index value is 5.83 which is a mean decrease of 0.66 from the May index value.

Relative numbers of males and females also change seasonally, and parallel the change which occurs at Nordegg. The ratio of males and females in May is 1 to 1 (15 males and 16 females), while in August there are approximately three times as many males as females (26 males and 8

females). This difference however is not statistically significant.

5.33 Crimson Lake (Fig. 39)

The histogram for specimens collected at Crimson Lake in 1961 shows a mainly duodecimguttata population. Two specimens have index values of 2 and 3 and are probably hybrids. The mean index is 6.50.

The range of index values for 1962 is 3 to 7 with the mean value at 6.53. The average index change from 1961 to 1962 - 0.03 - is quite small.

In 1963 the mean value decreased by 0.19, and the range in index values is 0 to 7. The population sample however is largely a duodecimguttata one much like those of the two previous years. The major difference is that oregona specimens are present in the 1963 series, but they are rare.

From May to August a general decrease occurred in the mean index values of the Crimson Lake samples. This seasonal index change corresponds with that of Nordegg and Rocky Mountain House.

Ten males and 23 females in May, 21 males and 17 females in July, and 25 males and 20 females in August were collected in 1963. The sex ratio is two females to one male in the May sample, but is one to one for July and August.

5.34 Lodgepole - eight miles south (Fig. 40)

In 1963, two small series of 19 and 17 specimens were collected at this locality in July and August respectively. Seasonal differences

between the two samples do not coincide with those of Nordegg, Crimson Lake, and Rocky Mountain House but the samples are probably too small to indicate real differences. However there seems to be a shift from a lower average index value earlier in the season to a higher average value later in the season. Both samples consist mainly of duodecimguttata specimens, but with a few hybrids.

The males and females are present in about equal numbers in both population samples, with nine females and 10 males taken in July, and nine females and eight males collected in August.

5.4 Notes on mating

During the summer of 1962, in the Nordegg area, 26 pairs of mating tiger beetles were collected. This is a phenotypically varied group, including both parental species and hybrids. Hybrid indices were determined for the specimens. Then, a chi square test for independency was applied to find out if specimens of a particular index more often selected a mate of the same index value. It showed that mating was non selective.

On several occasions I have taken repanda specimens in copulation with oregona and duodecimguttata individuals, but no hybrids have been found. It is doubtful that gene exchange takes place between repanda and oregona or duodecimguttata, to the extent that occurs between oregona and duodecimguttata.

5.5 Discussion

The kind of hybridization between oregona and duodecimguttata can be classified as one of introgression (Anderson 1949), and secondary intergradation (Mayr 1942). Introgression, as described by Anderson, is the incorporation of genes of one species into the gene complex of another species. Mayr states that secondary intergradation has occurred when "Two units, now connected by a steeply sloping character gradient were separated completely at one time and have now come into contact again after a number of differences have evolved." Mayr (1963) regards the species involved in this kind of hybridization as semispecies in that they show some of the characteristics of a species and some of subspecies. Many such cases have been described for birds, mammals, fish, amphibians and some invertebrates. These are too numerous to mention here but many are cited by Dobzhansky (1951), Mayr (1942, 1963), Mecham (1961), and Sibley (1961).

This section deals with historical aspects of the intergradation zone, width of the zone in connection with theories on origin of isolating mechanisms, and character displacement.

History.- The situation in western Alberta and northwestern Canada described above seems to be the result of secondary contact between the formerly isolated vicariant species oregona and duodecimguttata. Their phenotypic differences probably arose under different selective forces acting on allopatric populations. Breakdown of external barriers between them allowed their ranges to expand and come into contact. This has resulted in hybridization. Speciation of oregona and duodecimguttata was probably initiated in early Pleistocene times, but the process has not been completed. Climatic changes during the Pleistocene undoubtedly had a profound

influence on the distribution of these two forms as it did on other North American animal species (see Blair 1951). Unlike the vertebrates, however, locations of refugia for these tiger beetles or their population movements during the Pleistocene are not known because of the lack of a fossil record. The history of this zone of secondary intergradation is therefore speculative, and is based on the present distribution of both species, and current concepts of events during the Pleistocene. During the early period of oregona subspeciation, populations of duodecimguttata were not present in western regions they now occupy. Shortly after the development of o. guttifera, perhaps during the latter half of the Prairie interglacial (Karlstrom, 1961), duodecimguttata reinvaded western Canada east of the Rocky Mountains. Because, at the present time, few southern populations of duodecimguttata reach the eastern front of the Rockies in Colorado and New Mexico, the present western limits are presumed to be the extent of the western limits of duodecimguttata during the late Prairie interglacial. If any hybridization did occur in Prairie times it took place where the two species are presently sympatric. However, any evidence of pre-Recent introgression would be masked by the present hybrid belt. Hybridization probably did not occur in southern regions during the Wisconsin glaciation since no indication of introgression is evident in southern populations.

Width of the intergradation zone and origin of isolating mechanisms.- The hybrid belt between oregona and duodecimguttata is widest in northwestern Canada and narrowest in western Alberta. Individual specimens of oregona and duodecimguttata exist in all areas of greatest variability

including the Norman Wells population where they are outnumbered by intermediates. Width of the zone of intergradation is recognized as spatial limits of extreme variation.

There does not seem to be any reduced viability or fertility in the hybrid tiger beetles and they are present in large numbers in the Norman Wells sample described above. A composite of isolating mechanisms, although hardly pronounced in southern populations of oregona and duodecimguttata, may have become more completely developed than in northern populations of the two species before they made contact. This may account in part for the varying width of the zone of intergradation between oregona and duodecimguttata.

Somewhat analogous is the intergradation zone of the European crows Corvus corone cornix and C. c. corone (Mayr 1942, pp. 265-266), and that of the North American grackles Quiscalus quiscula quiscula and Q. q. versicolor (Huntington 1952). Dobzhansky (1951) attempts to explain the irregular width of the intergradation belt of the crows. He suggests that oldest regions of the zone are narrowest where isolating mechanisms have had more time to become established. Mayr (1942) does not believe this explanation corresponds with the facts presented by Meise, who observed the width of the hybrid zone of Corvus is determined by local ecological factors. Further, narrow stretches of intergradation occur in both recent and older parts of the zone. Because in Quiscalus, Huntington (1952) observed no reduced viability or fertility in the intermediates, he feels Dobzhansky's explanation is inadequate in principle, and suggests that increased mixing due to migration, and selective forces favouring the intermediate in a rapidly changing environment are the two main factors

affecting the width of area of intergradation.

Because the width of intergradation zones is determined largely by isolating mechanisms, it is appropriate to discuss variation in the width of the tiger beetle hybrid zone in the light of two sets of theories on the origin of isolating mechanisms.

For several hypotheses natural selection is believed to be responsible for the promotion of isolating mechanisms. One representative hypothesis postulates that intermediates are of lowered fertility or viability compared to parental forms. From this it is argued that individuals which enter into mixed pairs will eventually be eliminated from both populations because the hybrids they produce are being selected against. In time, as isolating mechanisms are perfected, the zone of intergradation is contracted. This is essentially Dobzhansky's view.

A second hypothesis treats the origin of isolating mechanisms as an incidental by-product of genetic divergence in isolated populations (Muller, 1940) rather than as the direct result of selection for reproductive isolation. Mayr (1963) points out that many isolating mechanisms vary geographically.

Because many isolating mechanisms have ecological components, any ecological changes in the incipient species are certain to affect their isolating mechanisms. The narrowness of the zone in western Alberta can be due in part to different habitat preferences (see Sec. 5.21, eight miles south of Lodgepole, and Crimson Lake). Sand with organic material, clay or mud seem to be preferred by duodecimguttata, while soils of pure sand or clean gravel are typical oregona habitat. In the north, where the

intergradation zone is wider, both species may be more broadly adapted. The broader northern zone may also be an effect of better adaptation of intermediates to the northern environment than to that of the south. However, in order to understand this zone of intergradation more completely ecological investigations should be undertaken.

Character displacement.- The elytral pattern of duodecimguttata is complete in western parts of the species range but it is reduced in eastern and southern regions. The full pattern also appears in the zone of intergradation. Eastern duodecimguttata specimens often have oregona - like elytral markings (see duodecimguttata taxonomic section 4.41). This situation may be interpreted as sympatric character divergence, which may be described as follows. Two closely related species of animals overlap geographically. Their differences are emphasized in areas of sympatry so that both species are easily recognized. In ranges where one of the species occurs alone it closely resembles the other species.

For several reasons it is doubtful that the variation in the elytral pattern of duodecimguttata is evidence of character displacement. Some workers observe that character displacement occurs within regions of overlap (Wilson and Brown 1956, Mayr 1963). The complete elytral pattern of duodecimguttata is present in the hybrid belt in western Alberta but it is also characteristic of populations far beyond the zone of overlap (Fig. 17). In addition variation in elytral pattern of duodecimguttata is not complimented by similar clines of other characters. For example the shape of the median lobe of the male is uniform throughout the range of duodecimguttata except in the hybrid zone where there are many intermediate shapes ranging from oregona to duodecimguttata (see

Sec. 3.3). Nowhere outside of the hybrid zone does the median lobe of duodecinguttata assume the shape of that of oregona. The same applies to the presence of hairs on the frons, top of the head, and post genae of duodecinguttata. The hairs are universally present throughout the species range except in the area of intergradation. Furthermore, since in the zone of hybridization, random interspecific mating takes place, it is presumed the difference in markings does not serve as an isolating mechanism.

TABLE 15. - Values assigned to diagnostic characters of specimens of Cicindela duodecimguttata and C. oregona for use in determination of compound character indices.

Elytral markings and areas of head	Values		
	2	1	0
Humeral lunule	complete	broken	two dots
Marginal band	complete	broken or trace	absent
Apical lunule	-	complete	two dots
Frons	-	hairy	glabrous
Post gena		hairy	glabrous

6. PHYLOGENY AND ZOOGEOGRAPHY OF THE NORTH AMERICAN SPECIES OF THE MARITIMA GROUP

6.1 Phylogeny

The ancestral form of the North American species of the maritima group is necessarily reconstructed from features that are widespread among extant species because no fossils are available. The rationale and principles used in re-constructing the characters of the hypothetical ancestor are explained in Cain and Harrison (1960). The characters of the ancestral species were probably as follows: dorsum, brown, opalescent; venter, metallic blue-green; thoracic pleura, copper colored; humeral, apical, and middle lunules, and marginal band, complete; lunules narrowly expanded as shown by hirticollis or repanda; shapes of the individual markings like those of repanda; hairs present on the head between the eyes; features of the male genitalia as they are now; flanges of the median lobe comparatively narrow like those of hirticollis or repanda; fields a, b, and c of the internal sac lightly aculeate; sclerites 1, 2, 3, 4 and 6 of the internal sac general size and shape of extant species; sclerite 5 large like those of hirticollis and repanda; sclerite between 2 and 6 intermediate size between that of oregona and hirticollis; pronotum of the larva densely pilose. The species was a riparian form, and it gave rise to three lineages (Fig. 45).

The first derivative stock (1) was perhaps characterized by an alteration of the elytral pattern in which the posterior portion of the humeral lunule was produced obliquely towards the median line; within the male internal sac field a and sclerites probably became respectively

densely aculeate and considerably reduced; the pronotum of third instar larvae was probably quite pilose.

This primary stock ultimately gave rise to the species limbata, bellissima, theatina, and columbica. The species limbata and bellissima appear to be most closely allied. The subspecies limbata hyperborea, and bellissima each have the posterior tip of the humeral lunule extending almost to the middle band; sclerite 5 of the male internal sac has been lost in these species; the riparian habit was abandoned and both species are sand dune inhabitants. Beside the differences in shape of their median lobes, limbata is very hairy between the eyes and bellissima is less so. In this respect, bellissima has departed further from the ancestral stock than has limbata. The southern races of the latter species, however, have lost almost all of the dark pigment of the elytra.

The species theatina and columbica appear to be more closely related to each other than they are to the other two. A humeral lunule whose posterior tip is briefly extended is a diagnostic feature of theatina and columbica; a very large triangular sclerite has evolved between 2 and 6 of the male internal sac, and sclerite 5 has not completely disappeared. They differ mainly in two characters: theatina is densely hairy between the eyes and lives on sand dunes, while columbica is sparsely hairy between the eyes and has retained the riparian ancestral characteristic.

The proposed phylogenetic course for limbata, bellissima, theatina, and columbica is not presented in a dichotomous scheme in Fig. 45

because different arrangements can be devised on the basis of other similarities among the four species. Distribution of hairs on the head, condition of elytral pattern, color or ecological preferences each can be employed to erect a different hypothetical historical course but these would imply a greater amount of parallelism or convergence than is required in the scheme I have suggested.

The second lineage (2) is represented by the species hirticollis which is somewhat remotely allied to the other existing North American species of the maritima group. This form evolved: a humeral lunule the posterior tip of which is distinctly hook-shaped; a comparatively pronounced twirl in sclerite 4, and a very large sclerite between 2 and 6 of the male internal sac; and it has retained a densely pilose pronotum of the third instar larva.

The third ancestral stock (3) probably developed or retained a c-shaped humeral lunule; field a of the male internal sac remained lightly aculeate and sclerite 5 increased in size. Secondary setae probably sparsely covered the pronotum of the third instar larva; and the species was most likely riparian. This ancestral stock gave rise to the species repanda, depressula, oregona, and duodecimguttata.

The species repanda appears to be less closely related to the other three species than they are to one another. Within the male internal sac, sclerite 5 has become very well developed and the sclerite between 2 and 6 has been lost; repanda ranges across North America but no introgression is evident with the other three species in areas of sympatry.

Evolving from a repanda like ancestor, the stock which gave rise

to depressula developed a median lobe with broad flanges, lost most of the frontal hairs, and developed a modified pattern of white elytral markings, which at first were extensive but subsequently became much reduced. Also the ancestral brown color of the dorsum was replaced by blue and green in the stock which developed reduced markings, and in the east the lowlands were abandoned by this form for life high in the mountains. Simultaneously the larva of this derivative form lost most of the pronotal hairs characteristic of the pronotum of the ancestral stock.

Another derivative stock from a repanda like ancestor, was the progenitor of duodecinguttata and oregona. This stock developed at first slightly reduced elytral markings. Subsequently it became divided into two geographically isolated groups the western of which lost the frontal hairs, developed strongly reduced elytral markings, and throughout much of its range the brown color of the dorsum was replaced by green, blue, or purple, and the pleural sclerites became blue or green. The pronotum of the larva gradually lost much of the pubescence evident in the ancestral larva. This western isolate is the species oregona. In the eastern isolate, the elytral markings were also reduced, and blue and green color of the dorsum appeared. The mutations producing reduced markings became widespread replacing the ancestral condition throughout most of the range of the species. Hairs on the pronotum of the larva were reduced in number. This eastern isolate is the species duodecinguttata. Following a period of separation too short to permit the development of complete reproductive isolation the eastern and western stocks met one another and a narrow zone of hybridization

developed in the area of contact.

This scheme requires postulation of an appreciable amount of parallel evolution. Frontal hairs were lost or reduced four times. Green or blue color of the dorsum was developed six times. Broad flanges on the median lobe were developed six times. The primitive elytral pattern was lost five times, but by two different phyletic branches. In one of these extensive reduction of lateral pigmentation took place. The other type of pattern breakdown was developed by increased pigmentation.

Thus these species, together form a structurally uniform group in which a number of similar structures have arisen independently. This suggests that the group possesses a good degree of evolutionary homodynamy (Bock 1963). This principle is defined as follows: "The number of times and ease with which an identical or very similar feature may arise independently within a group depends upon its degree of evolutionary homodynamy which in turn depends upon its common genetical-developmental potential." In the light of this principle similar structures that have arisen independently in the North American maritima group are considered to be homologous in the broad sense, which is defined by Bock as follows: "homologous features (or conditions of the features) in two or more organisms are ones that can be traced back to the same feature (or condition) in a group possessing a high degree of evolutionary homodynamy."

6.2 Zoogeography

The following account of the development of the distribution of

the North American species of the maritima group is hypothetical. No related fossil species are available and extensive sympatry occurs among some extant widespread species. Movements, and times and places of origin of extant species are necessarily constructed on the basis of: distribution and morphological features of the species; geological and climatic events of the Tertiary and Pleistocene in North America; and rates of evolution in some other groups of insects.

Insects generally develop modifications of structural features at a slow rate. Many fossil species of the early or middle Tertiary closely resemble existing species (Linsley 1958, Ross 1958, Becker 1963, Quate 1963, Sabrosky 1963, and Sturtevant 1963). Most of these are members of recent genera. However, Zeuner (Sylvester - Bradley, 1963), by means of analysis of 212 species of fossil Apoidea, Lepidoptera, and Saltatoria, reckons that excepting the honey-bee all living species evolved in the Pleistocene. He estimates half to one million years is a reasonable time required for the evolution of a full species. Zeuner further notes that no insect species are known with certainty to have survived from the Miocene (see Zeuner 1943, for more information on the time factor in evolution of insects). There is no evidence of recent vigorous evolution within the North American species of the maritima group. Indeed these are rather primitive in comparison with other species groups of Cicindela. The ancestral stock of the maritima group may have been in existence during the early Tertiary. Living species may have evolved during the later Tertiary or early Pleistocene.

Historical events which may have effected geographical isolation and subsequent speciation of tiger beetle populations are of importance.

Thus it is necessary to review briefly geological and climatic changes in western North America during the Tertiary and Pleistocene (see Blackwelder 1948, King 1958, MacGintie 1958, Martin 1958, and Mengel 1964).

The Tertiary was marked by several periods of crustal disturbances. Early Tertiary was a time of extensive mountain building throughout the west, and it was then the initial Rocky Mountain system was thrust up. Crustal folding was renewed in the middle Tertiary (late Miocene). Gentle folding in the Rockies prevailed. Disturbances were evident in coastal and southeastern California, and southern Nevada, while other mountains were widely distributed throughout the American west. A chain of volcanoes was built up along the east flank of the Sierra Nevada and Cascade Mountains. Large basins were produced, many of which became lake basins. At the close of the Tertiary (late Pliocene) once again crustal folding occurred along the Pacific coast, and in Nevada and Utah. The modern California Coast Range, Wasatch and Ruby Mountains and many others were elevated during this period. The southwestern plateau was raised to its present level, and most of the interior drainage systems were renewed.

Early Miocene and most of the Pliocene were periods of relative quiet. Stream systems wore down western mountains to scattered hills, and extensive plains were formed on which large lakes drained or were filled.

The climate in early Tertiary was warmer than now. Tropical forests filtered into the north Temperate Zone while temperate conditions prevailed in Rocky Mountain regions. In the Miocene the climate became cooler and temperatures steadily decreased into the Pleistocene.

Simultaneously climatic zones moved southward and southwestern regions became drier.

The end of the Tertiary and beginning of the Pleistocene was characterized by the gradual development of mountain glaciers and continental ice masses. There were five major glacial stages in North America, the Nebraskan, Kansan, Illinoian, Iowan, and Wisconsin. Between these occurred long warm periods, the Aftonian, Yarmouth, Sangamon, and Prairie.

In glacial periods glaciers extended southward along mountain ranges. These gave rise to rivers which descended onto open basins where much sand and glacial till was deposited. Large lakes developed in nearly all western basins.

Climate and vegetation similar to those of the present time were prevalent in interglacial periods in northern latitudes.

All of the North American species of the maritima group live in subarctic to warm temperate regions. Perhaps the ranges of hirticollis and oregona extend for a short distance into Mexico but for the most part they are northern forms. The species hirticollis and repanda are almost transcontinental and inhabit regions from the Cascades in the west to the Atlantic coast. Ranging from the Atlantic seaboard to the eastern slopes of the Rockies duodecimguttata is the only true eastern form. Inhabiting areas from the Rocky Mountains to the Pacific coast oregona is the western counterpart of duodecimguttata. The species depressula is restricted to high elevation of the Cascade Range and Sierra Nevada, and in river valleys near the Pacific coast from northern California to

southern Alaska. The species limbata inhabits areas just east of the Continental Divide. Further south, however, populations are found in Kane County, Utah(l. albissima Rumpp). The ranges occupied by bellissima, theatina, and columbica are rather restricted: San Luis Valley in south-central Colorado is the entire range of theatina; bellissima occurs on sea beaches in western Oregon and southwestern Washington; while columbica exists in southeastern Washington on beaches of the Snake River.

Knowledge of the distribution of the North American species of the maritima group supports the premises that: the ancestral species was a cool adapted form, and mountain ranges of western North America are effective geographical barriers particularly the Rocky Mountain system.

The relationships of the Nearctic species of the maritima group to those of the Old World members are not understood (but see Papp 1952), so speculation on time and direction of intercontinental movements is not warranted. However it seems certain that such movements did occur, probably by way of a Bering land bridge (see Gressitt 1963). The hypothesis which follows is based on the as yet unestablished premise that all the Nearctic species are more closely related to one another than to any Palearctic species.

The primitive ancestor of the North American species of the maritima group may have inhabited cool-temperate regions of North America in late Miocene. By virtue of its habits it may have filtered southward along alpine river systems near revived mountains of western

North America. It may have assumed a reticular distribution among these mountains and in cooler regions further east. By the continuous folding of strata, and volcanic eruptions, populations probably became disjunct and geographically isolated. The first three derivative stocks may have been established during the course of this unsettled period.

Very little can be said about the place of origin and geographical movements of hirticollis because of its present vast range and widespread sympatry with repanda, oregona, and duodecimguttata. It is probably a relatively old form.

The derivative stock, that gave rise to limbata, bellissima, columbica, and theatina, may have ranged throughout cooler regions of western North America up to the late Pliocene. Western North America had been worn down to extensive plains. Mountains were no longer effective geographic barriers, and sandy habitats occurred abundantly near the coast, near lakes and rivers, and in dry areas remote from water. Perhaps during its existence the ancestral species became more generally adapted and improvements of functions allowed it to inhabit sandy environments in arid regions, but it also continued its riparian habits. The renewed crustal unrest of the later Pliocene probably disbanded and isolated populations, that evolved into limbata, bellissima, and theatina.

The species limbata may have developed as a sand dune inhabitant on the northeastern side of the revived Rocky Mountains in late Pliocene or early Pleistocene. The original form probably resembled the boreal subspecies 1. hyperborea. Southern populations were probably established

during cooler glacial periods. See Rumpp (1961), for some ecology and mechanism of loss of elytral pigmentation in southern populations of limbata.

The ancestral stock of bellissima, probably became isolated on the Pacific coast by the renewed folding of the Coast Range in late Pliocene or early Pleistocene.

Populations that evolved into columbica probably became locked in by the Sierra Nevada and Rocky Mountains perhaps in the early Pleistocene. Within this area it retained the riparian habits of the ancestral stock.

The species theatina may have originally been isolated from other related populations to the east of the Continental Divide in Colorado. It perhaps had a greater range than the San Luis Valley to which it is now restricted.

The ancestral stock from which repanda, depressula, oregona, and duodecimguttata evolved may have originally been isolated to the east of the Rockies. It eventually became transcontinental, probably in early Pliocene.

The place and time of origin, and subsequent geographical distributions of repanda is obscured because it ranges throughout most of north temperate North America and is sympatric with several related species, and perhaps speciated before late Pliocene.

The species depressula may have developed in late Pliocene. Primitive populations of depressula, represented by d. eureka, on the

west side of the Cascade Range and northern Sierra Nevada probably became geographically segregated from the form which gave rise to duodecinguttata and oregona.

The common ancestor of the species duodecinguttata and oregona probably occupied the entire cool temperate North America during the middle Pleistocene. The extant species may have been formed during middle Pleistocene. Dissection of the range of the ancestral stock took place in glacial periods of the later Pleistocene when ice masses covered Canada and glaciers spread southward on high mountain ranges. The species duodecinguttata evolved in the east and oregona in the west with the Rockies acting as the major geographical barrier. In glacial periods it is doubtful that populations of duodecinguttata merged with those of oregona in southeastern regions of the Rockies for no evidence of that exists. Hybridization between these species is proof of their close relationship and that their reproductive isolating mechanisms have not yet become fully developed. Perhaps hybridization between them was more extensive in earlier interglacial periods and their isolating mechanisms have become gradually more effective with each successive glacial period.

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FIG. 1 - Median lobe and inverted internal sac of Cicindela duodecimguttata.
1a, dorsal aspect; 1b, left lateral aspect; 1c, apical portion, dorsal aspect. a, field a; b, field b; c, field c; 1, sclerite 1; 2, sclerite 2; 3, sclerite 3; 4, sclerite 4; 6, sclerite 6.

FIG. 2 - Median lobe and inverted internal sac of Cicindela oregona.
2a, dorsal aspect; 2b, left lateral aspect; 2c, apical portion, dorsal aspect. 5, sclerite 5.

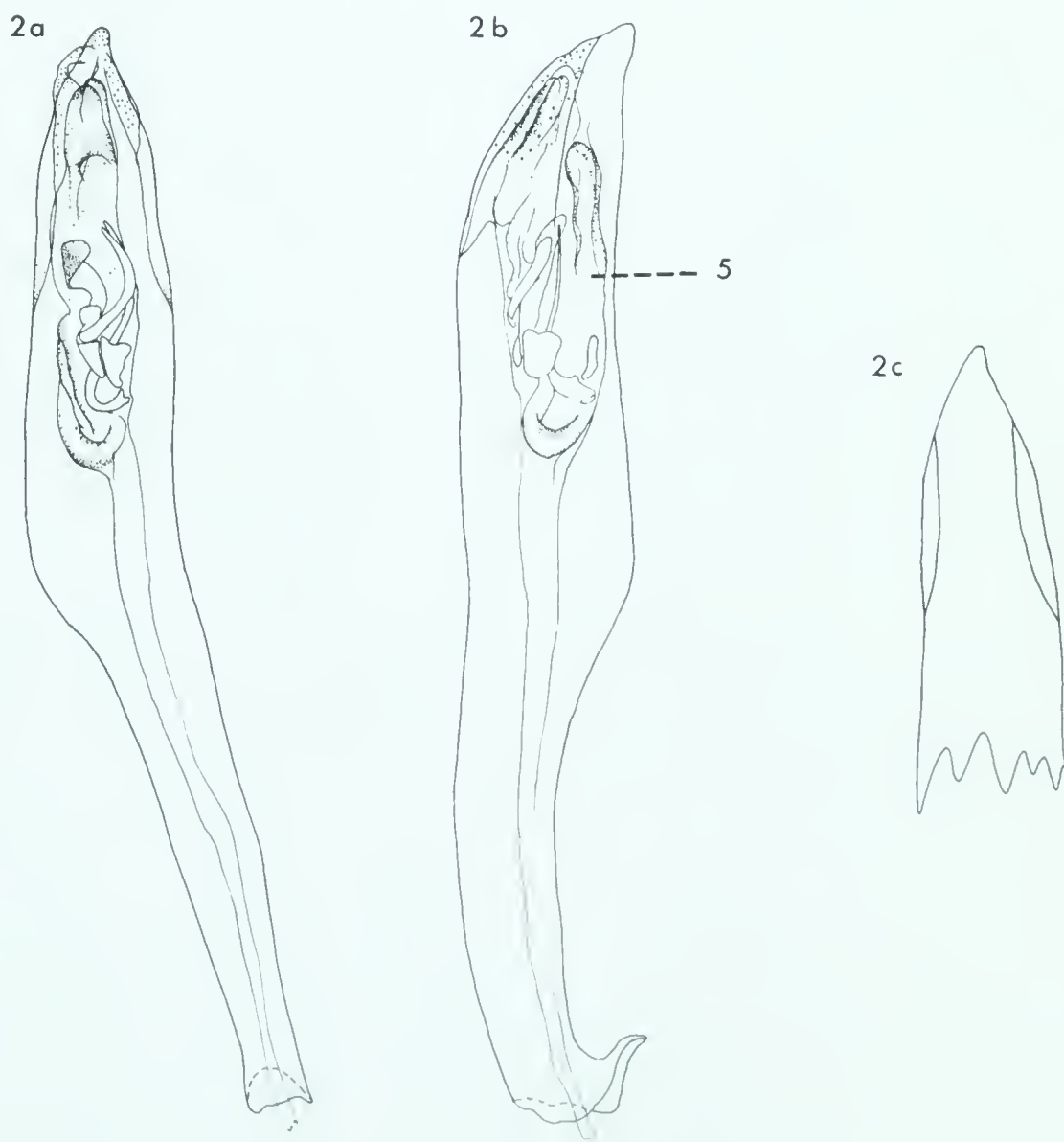
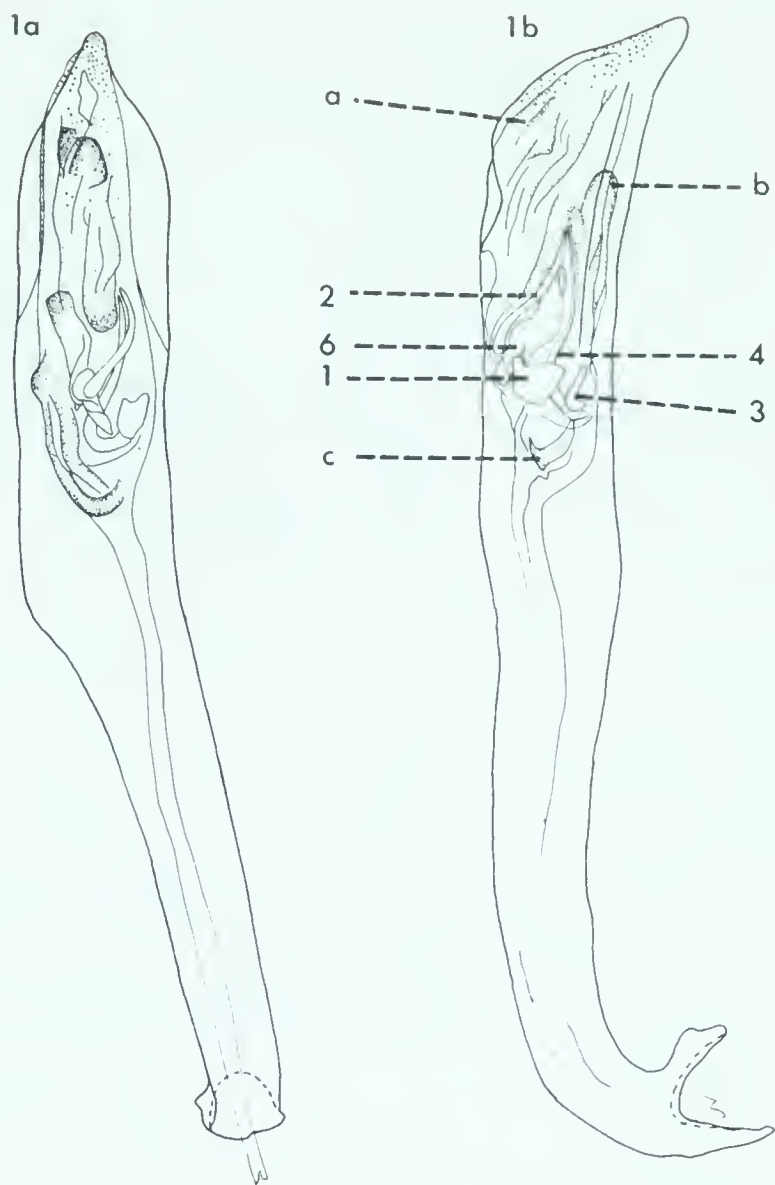


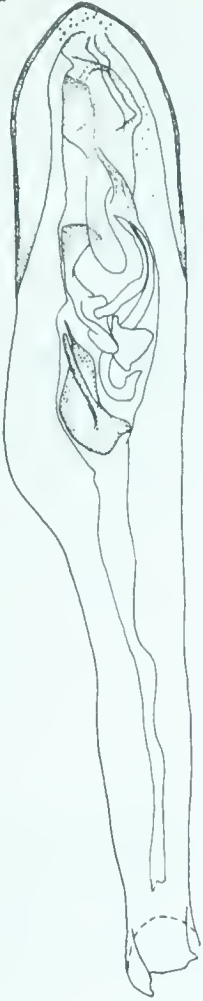
FIG. 3 - Median lobe and inverted internal sac of Cicindela depressula.

3a, dorsal aspect; 3b, left lateral aspect; 3c, apical portion,
dorsal aspect.

FIG. 4 - Median lobe and inverted internal sac of Cicindela repanda.

4a, dorsal aspect; 4b, left lateral aspect; 4c, apical portion,
dorsal aspect.

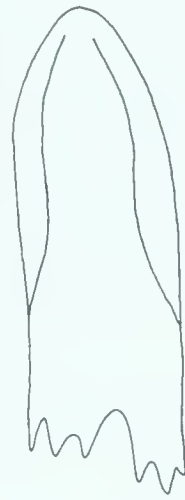
3a



3b



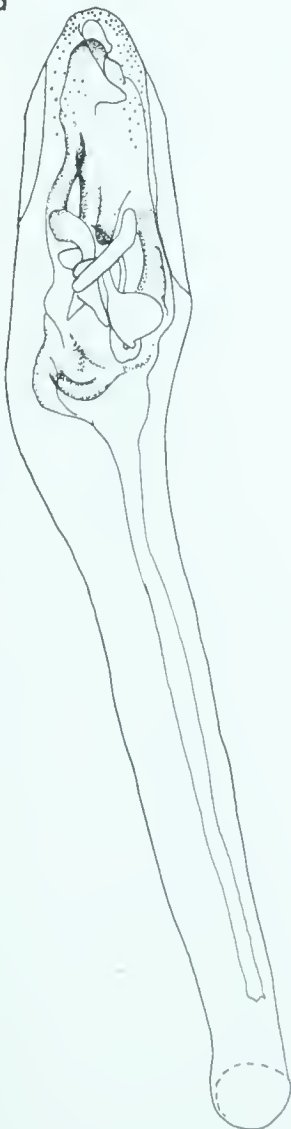
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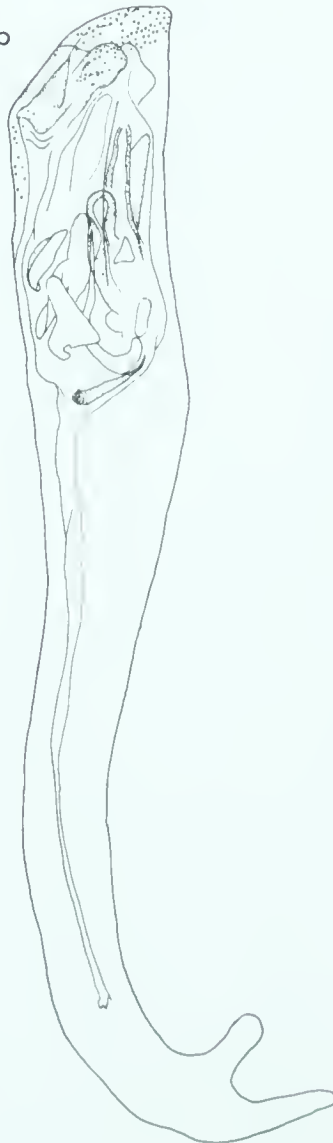
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4a



4b



4c



FIG. 5 - Median lobe and inverted internal sac of Cicindela limbata.

5a, dorsal aspect; 5b, left lateral aspect; 5c, apical portion,
dorsal aspect.

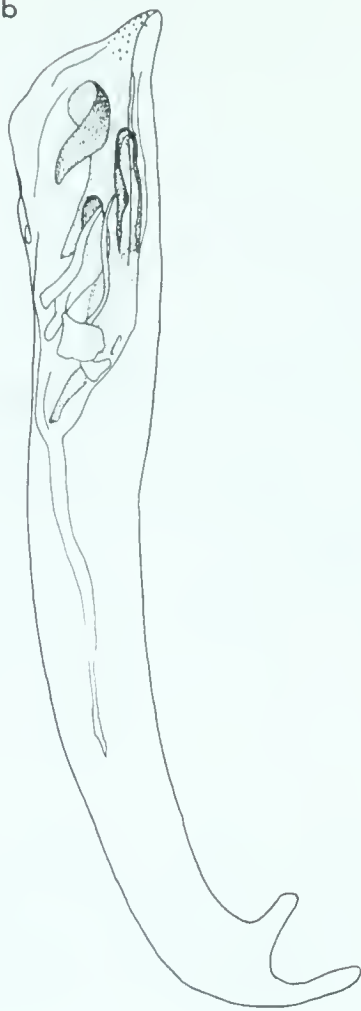
FIG. 6 - Median lobe and inverted internal sac of Cicindela bellissima.

6a, dorsal aspect; 6b, left lateral aspect; 6c, apical portion,
dorsal aspect.

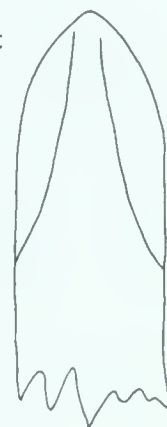
5a



5b

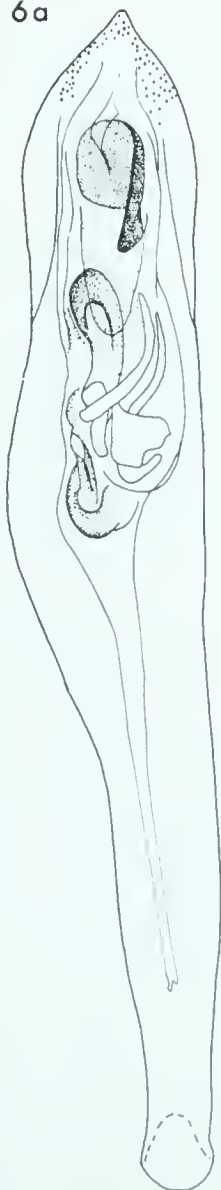


5c



1 mm

6a



6b



6c

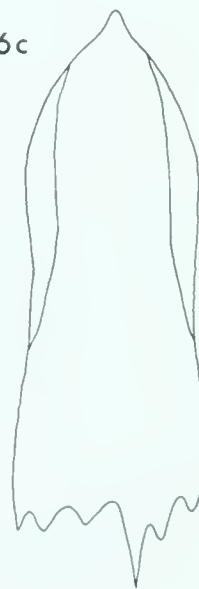


FIG. 7 - Median lobe and inverted internal sac of Cicindela columbica.

7a, dorsal aspect; 7b, left lateral aspect; 7c, apical portion,
dorsal aspect.

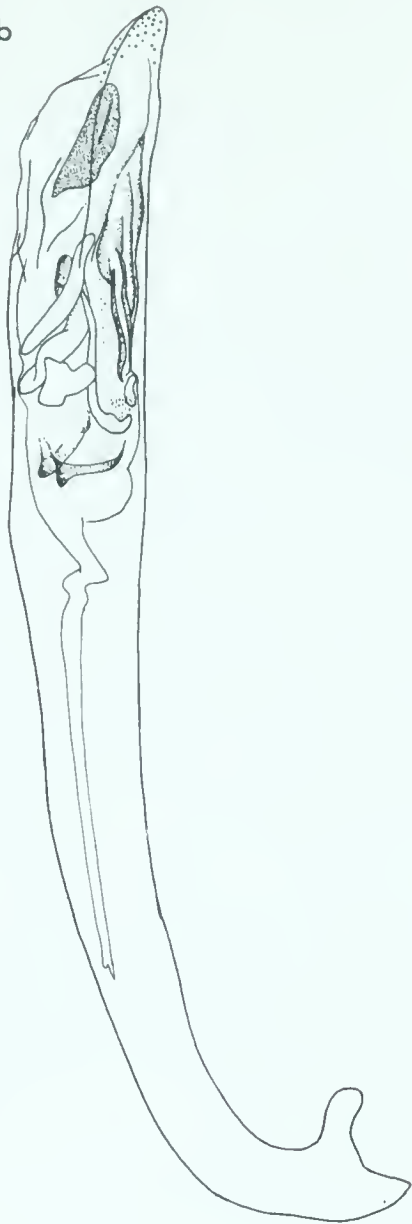
FIG. 8 - Median lobe and inverted internal sac of Cicindela hirticollis.

8a, dorsal aspect; 8b, left lateral aspect; 8c, apical portion,
dorsal aspect.

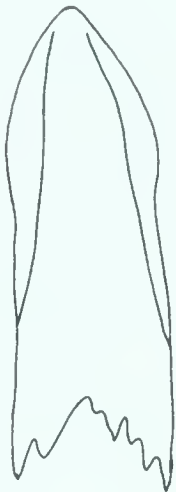
7a



7b



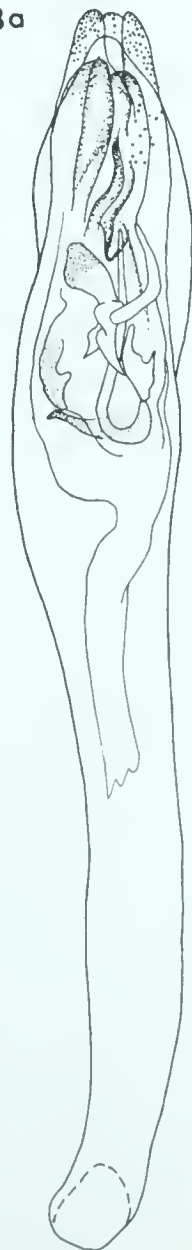
7c



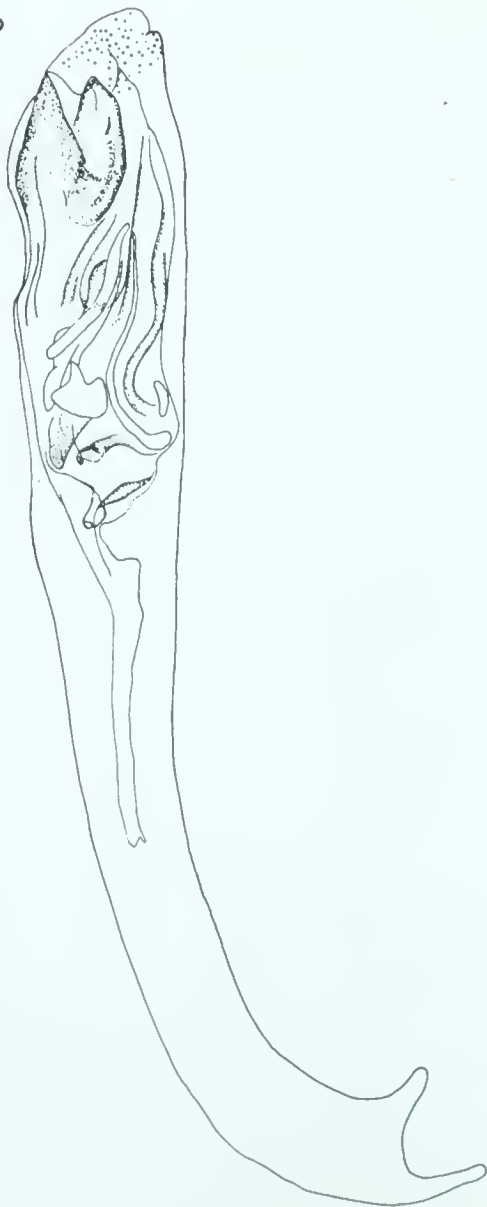
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8a



8b



8c

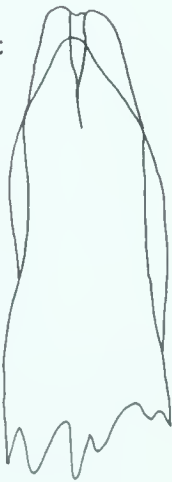
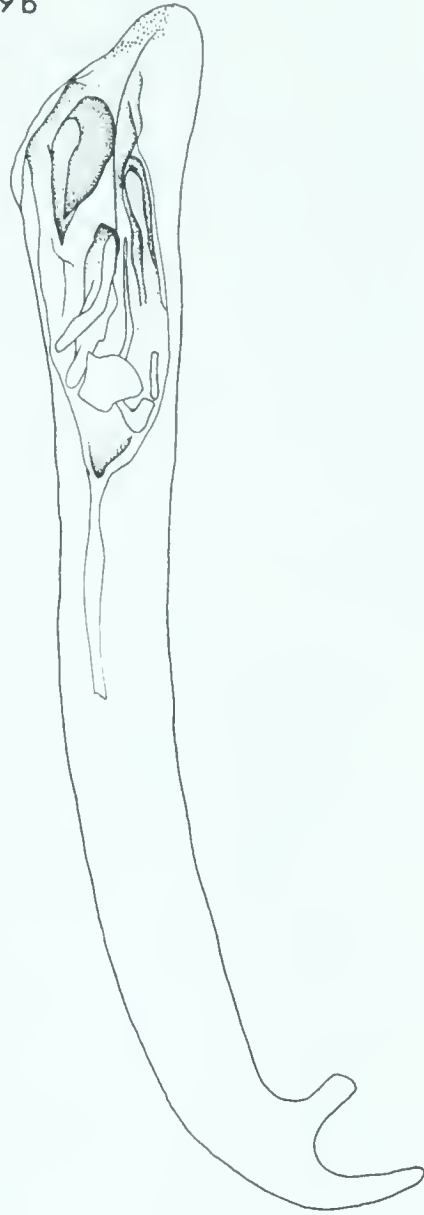


FIG. 9 - Median lobe and inverted internal sac of Cicindela theatina.
9a, dorsal aspect; 9b, left lateral aspect; 9c, apical portion,
dorsal aspect.

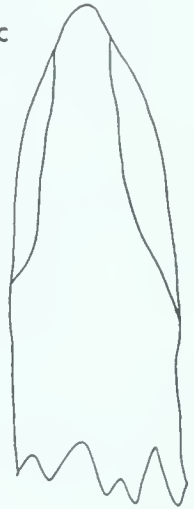
9a



9b



9c



1mm

FIG. 10 - Sclerites of the internal sac of the

North American species of the maritima group.

Sclerites numbered as in FIG. 1. Magnification
is 62.5x.




















































	C.duodecimguttata	C.oregona	C.depressula	C.repanda	C.limbata	C.bellissima	C.columbica	C.hirticollis	C.theatina
1									
2									
3									
4									
5									
6									

FIG. 11 - Anterior view of the head of C. duodecimguttata showing the presence of hairs on the frons and between the eyes.

FIG. 12 - Anterior view of the head of C. oregona showing the restricted distribution of hairs near the inner edge of each eye.

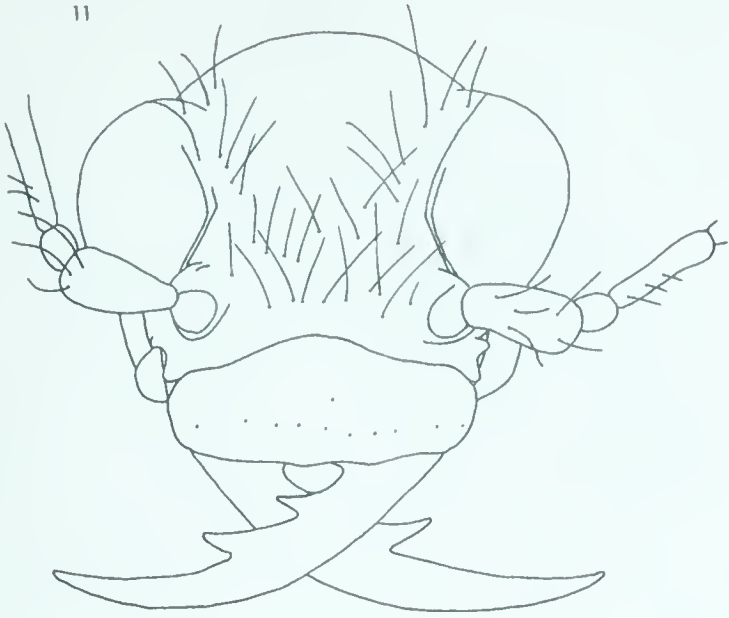
FIG. 13 - Lateral view of the head of C. duodecimguttata showing hairs on the post gena.

FIG. 14 - Lateral view of the head of C. oregona showing the glabrous post gena.

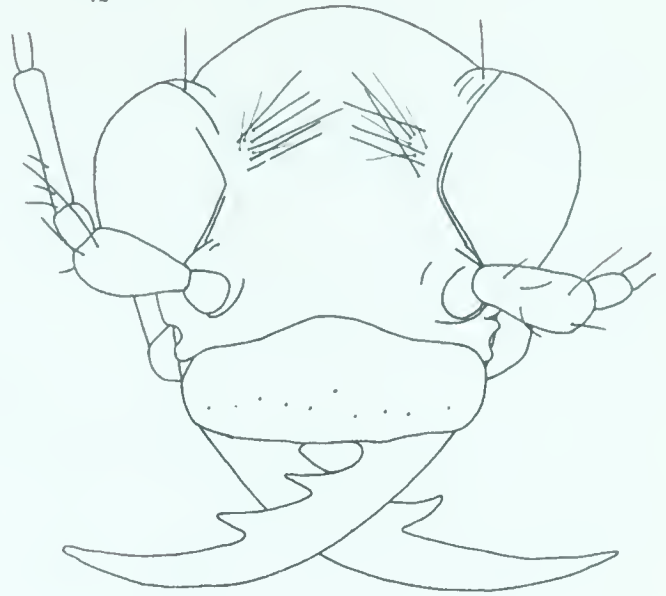
FIG. 15 - Left elytron of C. duodecimguttata with explanation of terms used in the text: HL, humeral lunule; MAR, marginal band; MID, middle band; AL, apical lunule.

FIG. 16 - Left elytron of C. oregona.

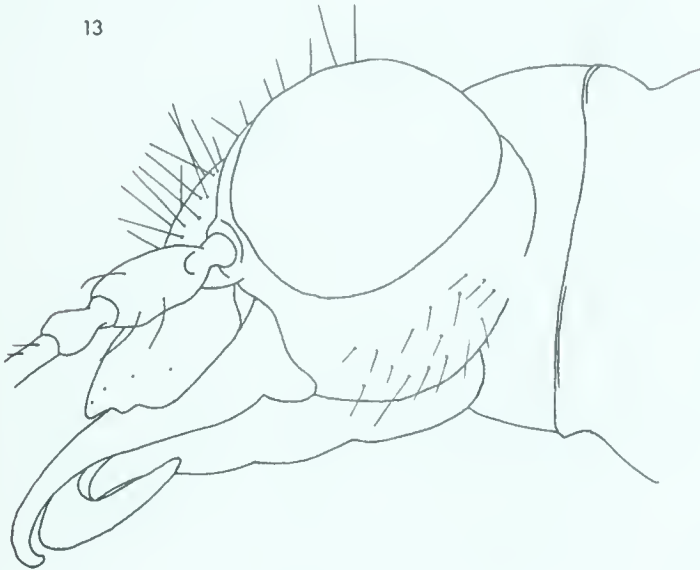
11



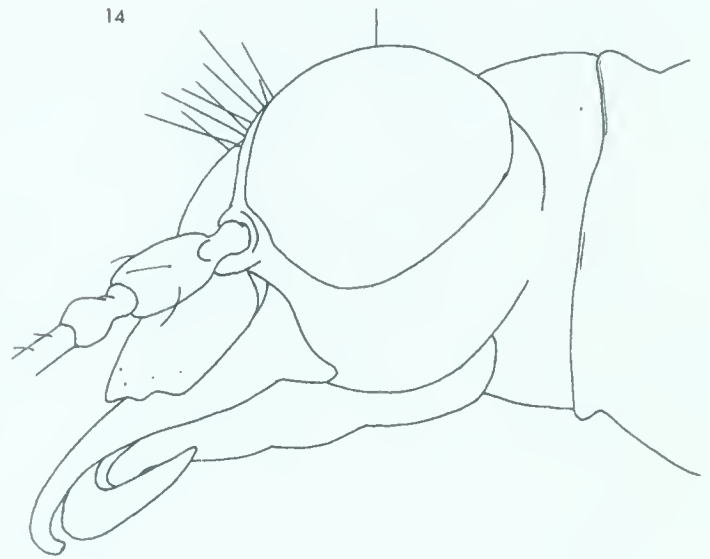
12



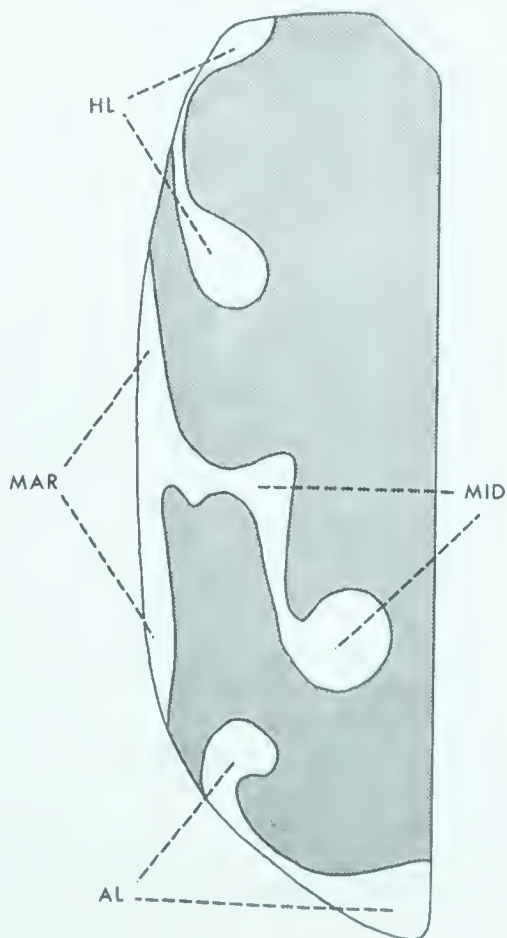
13



14



15



16

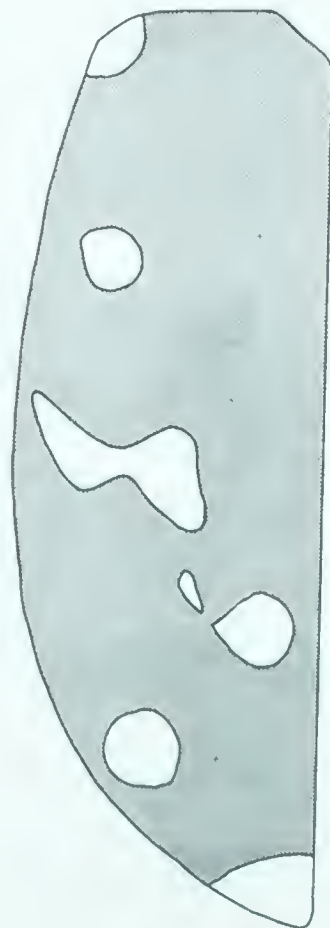


FIG. 17 - Distribution map of C. duodecimguttata and
average compound character index values for 18
population samples.

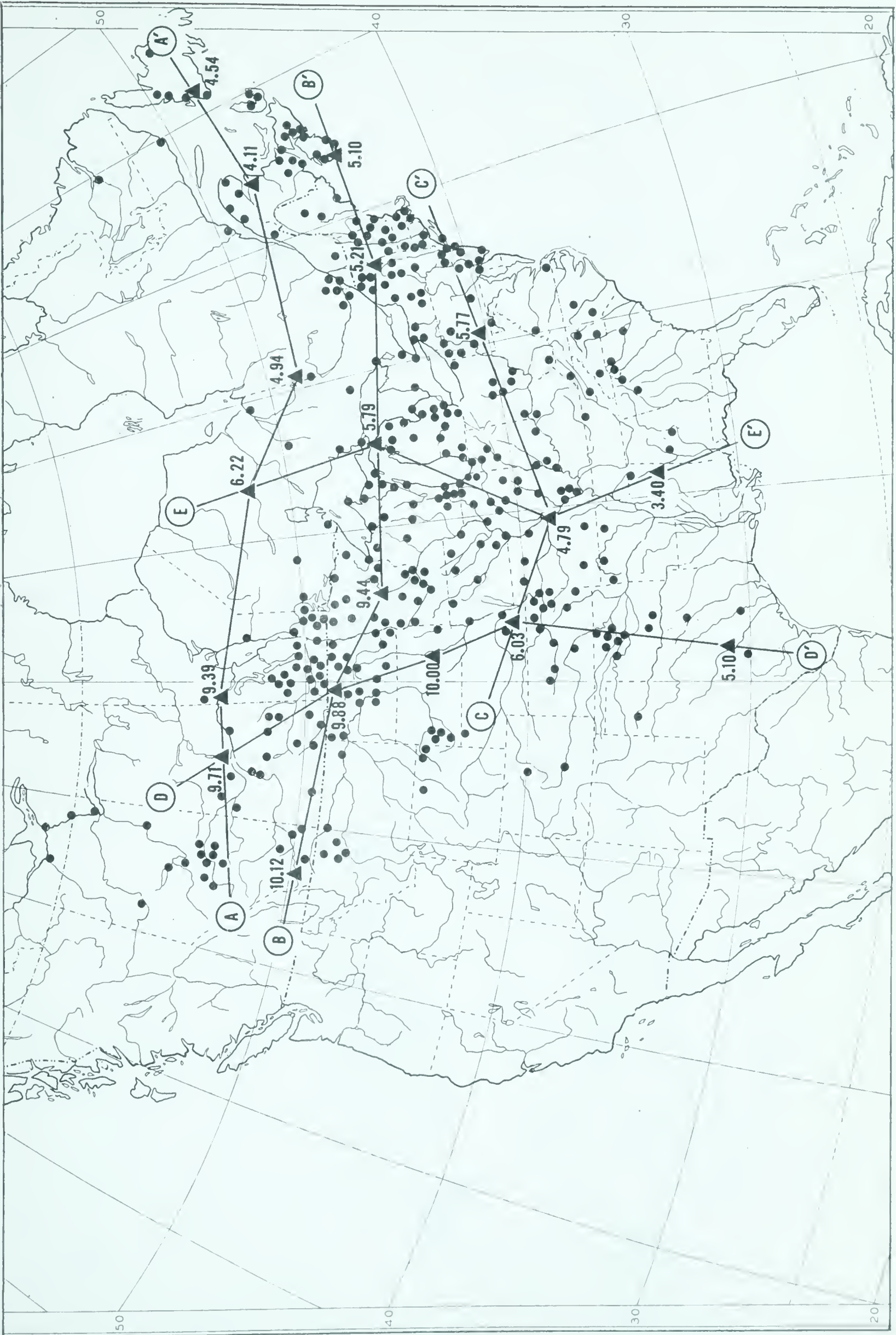


FIG. 18 - Geographical distribution of the subspecies of C. oregona.

Legend:

C. o. oregona - black disc

C. o. guttifera - circle with black disc in centre

C. o. maricopa - star

C. o. navajoensis - triangle

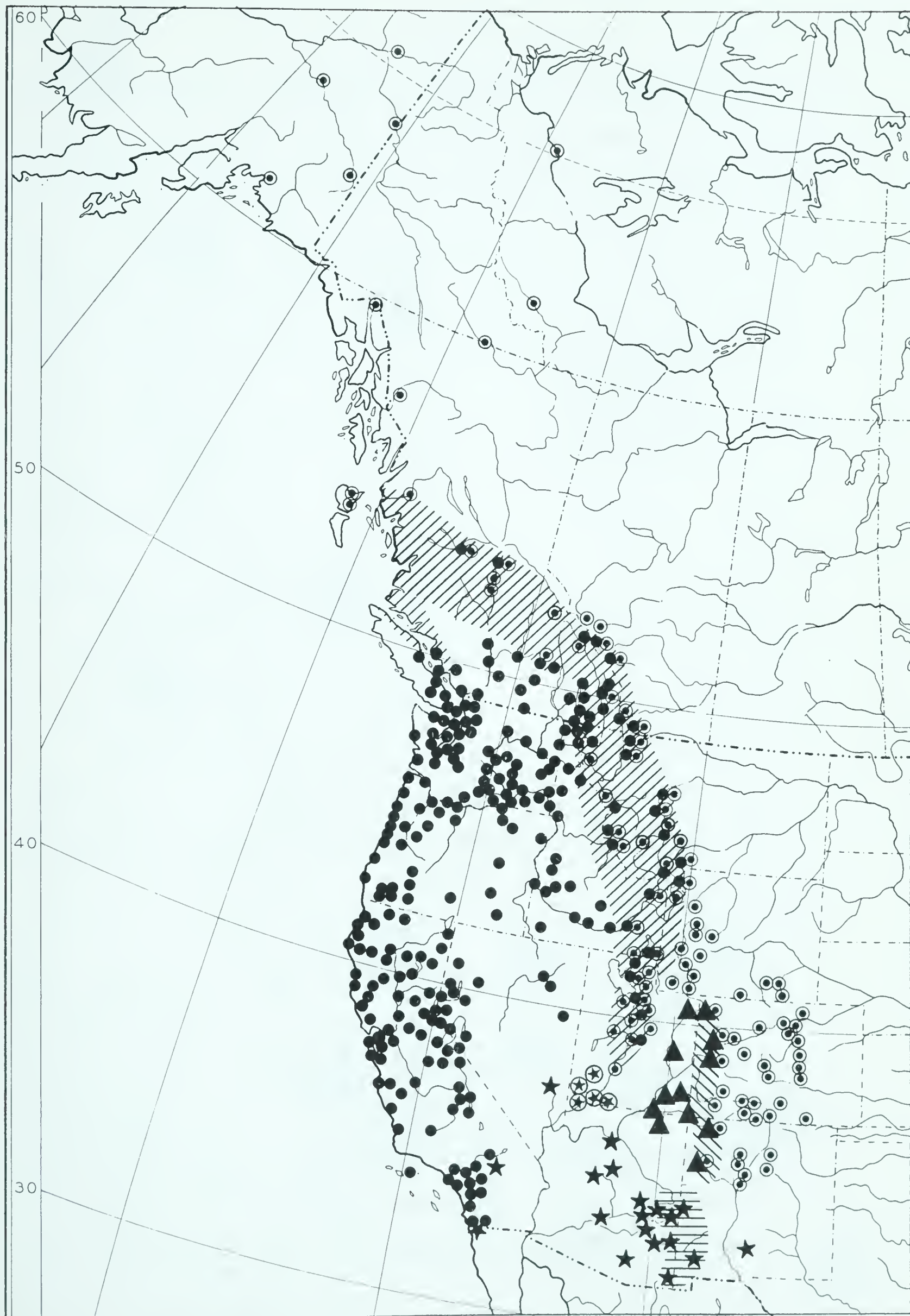
C. o. maricopa x o. guttifera - circle with star

oregona x guttifera, hybrid zone - vertical lines slanted to right

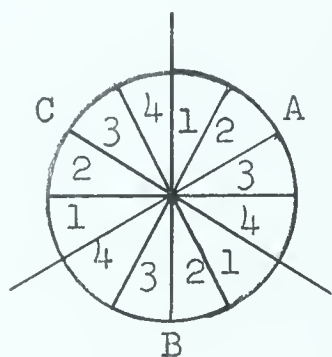
guttifera x navajoensis, hybrid zone - vertical lines slanted to left

maricopa x navajoensis, hybrid zone - horizontal lines

Both parental forms are present at a location when two different symbols are joined together.



Legend for the pie-graph symbol:



Elytra	Color	Thoracic pleura	Color
A	brown	1	coppery
B	green	2	metallic green
C	blue	3	metallic blue
		4	metallic purple

Localities of population samples are denoted by the geographical position of their pie-graph symbols and every member of the sample appears on the pie-graph. The total number of specimens that have the same color combination is indicated opposite the correct pie-section. Thus number 20 placed adjacent to 1 in section A signifies that 20 specimens of the population sample have coppery thoracic pleura and brown elytra.

Legend for localities:

A - Tanana River, Alaska	H - Kootenay P., Alta.	O - Athalmer, B.C.
B - Haines, Alaska	I - Banff, Alta.	P - Oliver, B.C.
C - Watson L., Yukon	J - Glacier N.P., Mont.	Q - Vernon, B.C.
D - Terrace, B.C.	K - Helena, Mont.	R - Vancouver, B.C.
E - Ft. Fraser, B.C.	L - Pullman, Wash.	S - Garibaldi Pk., B.C.
F - Cinema, B.C.	M - Spokane, Wash.	T - Victoria, B.C.
G - Q. Ch.Islands, B.C.	N - Creston, B.C.	U - Seattle, Wash.

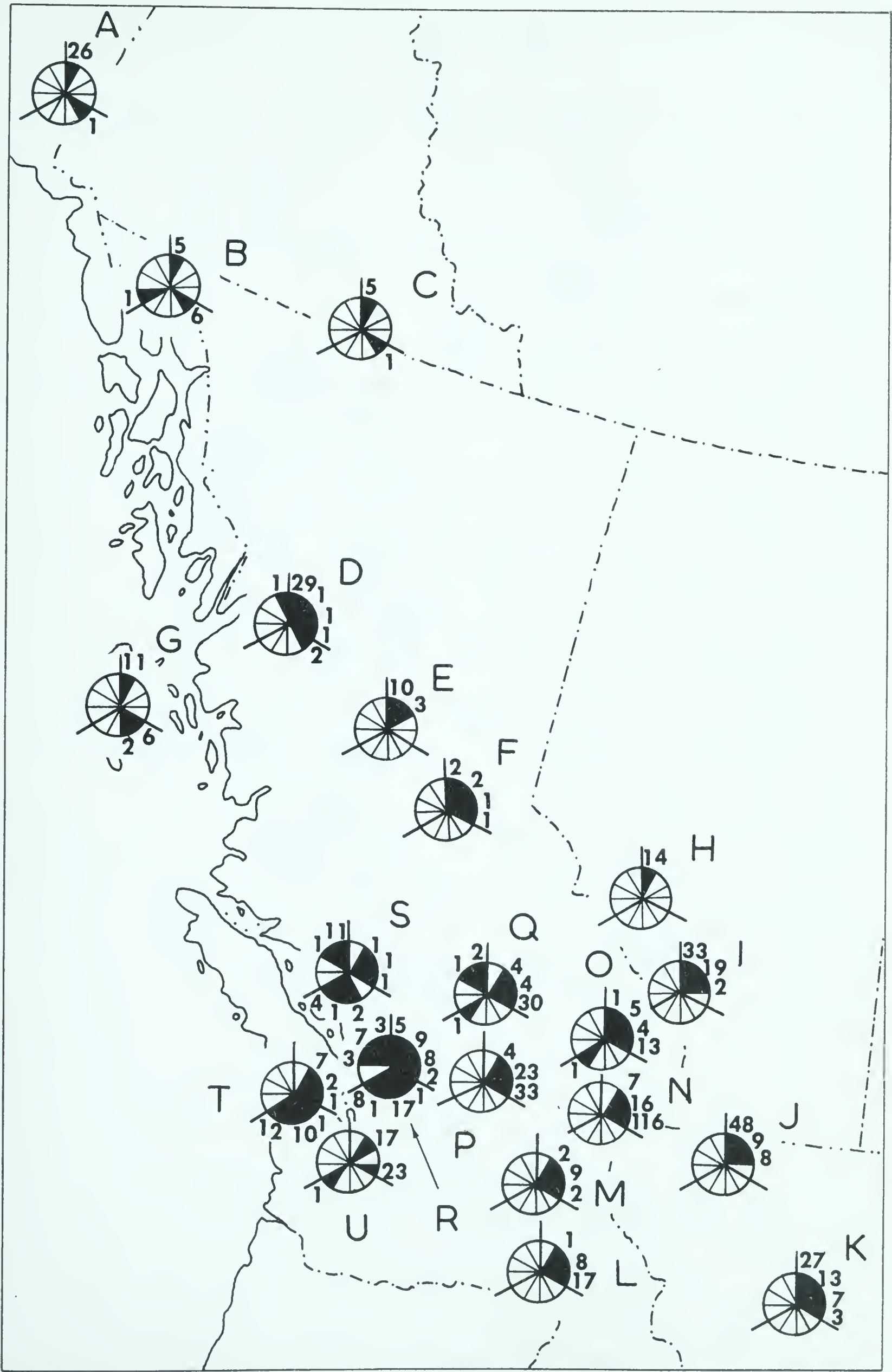


FIG. 20 - Pie-graph map illustrating geographic color variation in elytra and thoracic pleura of some population samples of Cicindela oregona.

Legend for the pie - graph symbol: same as for FIG. 19.

Legend for localities:

Oregon: A - Portland; B - Hood River and Dalles; C - Umatilla; D - Florence; E - Charleston; F - Port Orford and Humbug Mountain; G - Medford; H - Eugene; I - Lake Albert; J - Steens Mountain; K - Malheur Lake; Idaho: L - Owyhee County; California: M - Gottville; N - Dillon Creek; O - Eureka and Trinidad; P - Hoopa Valley; Q - Douglas; R - Bridgeville and Mad River; Miranda and Fort Deward; T - Lassen National Park; U - Lake Tahoe; Nevada: V - Walker Lake; California: W - Bucks Lake; X - Chico; Y - Sacramento; Z - Cloverdale a - San Francisco; b - Antioch; c - Yosemite National Park; d - Bigpine; e - Lone Pine and Olancha; f - Coalinga; g - Carmel; h - Santa Cruz Island; i - Los Angeles; j - Colton; k - Victorville; l - San Jacinto Mountains; m - San Diego; n - Plumas County.

FIG. 21 - Locality map of population samples of
C. oregona LeConte compared in scatter diagrams.

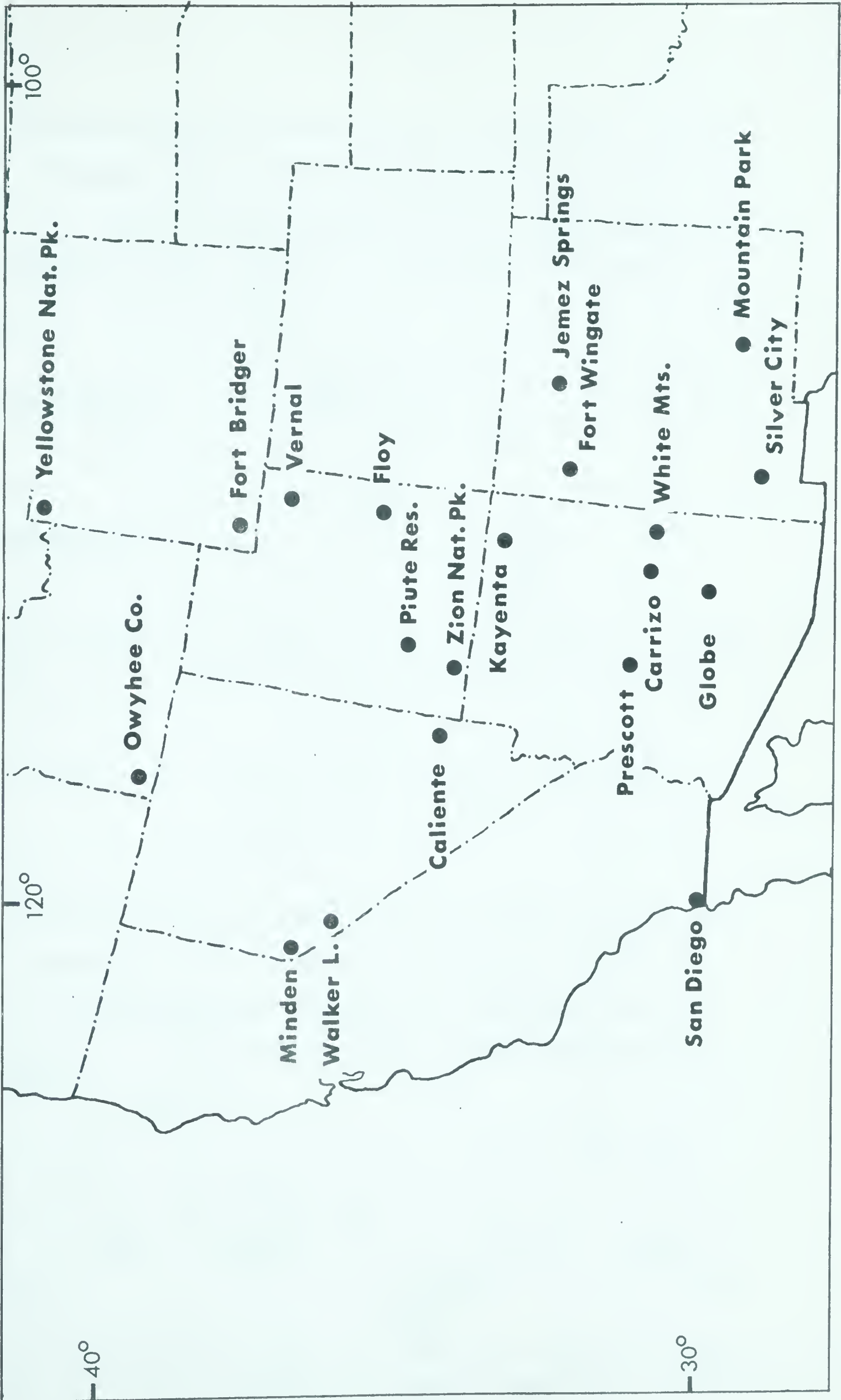




FIG. 22 - Pictorialized scatter diagram illustrating character differences between population samples of male Cicindela oregona oregona and male Cicindela oregona maricopa.

Explanation of symbols: Black triangles - oregona maricopa

Small - Prescott, Arizona

Large - Caliente, Nevada

Inverted triangles - oregona oregona

Small - Owyhee County, Idaho

Large - Minden, Nevada

Hexagons - specimens of an intermediate population

- San Diego, California

Vertical bar - color of elytra. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

Horizontal bar - color of thoracic pleura. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

FIG. 23 - Pictorialized scatter diagram illustrating character differences between sample populations of female Cicindela oregona oregona and female Cicindela oregona maricopa.

Explanation of symbols: same as for FIG. 22.

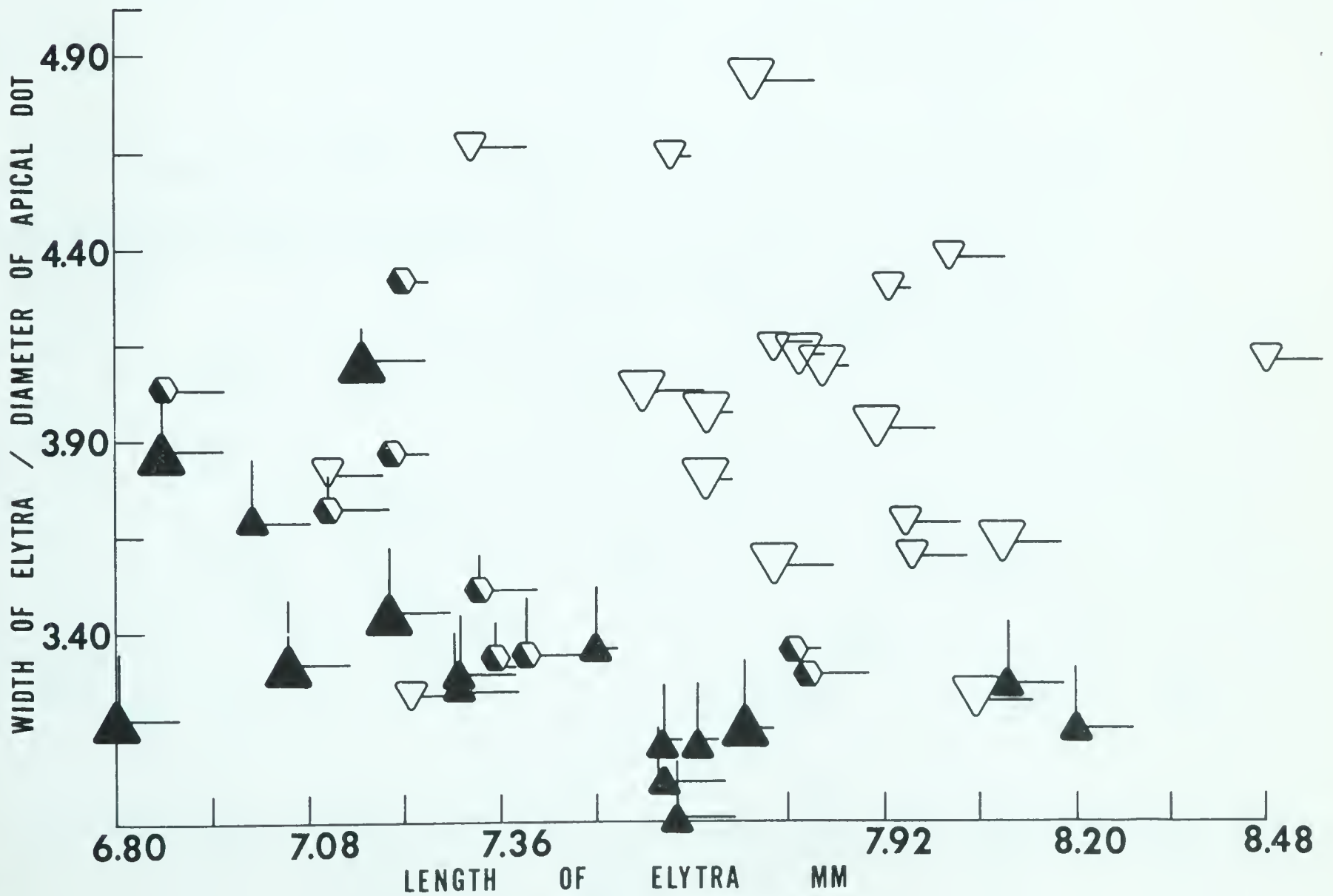
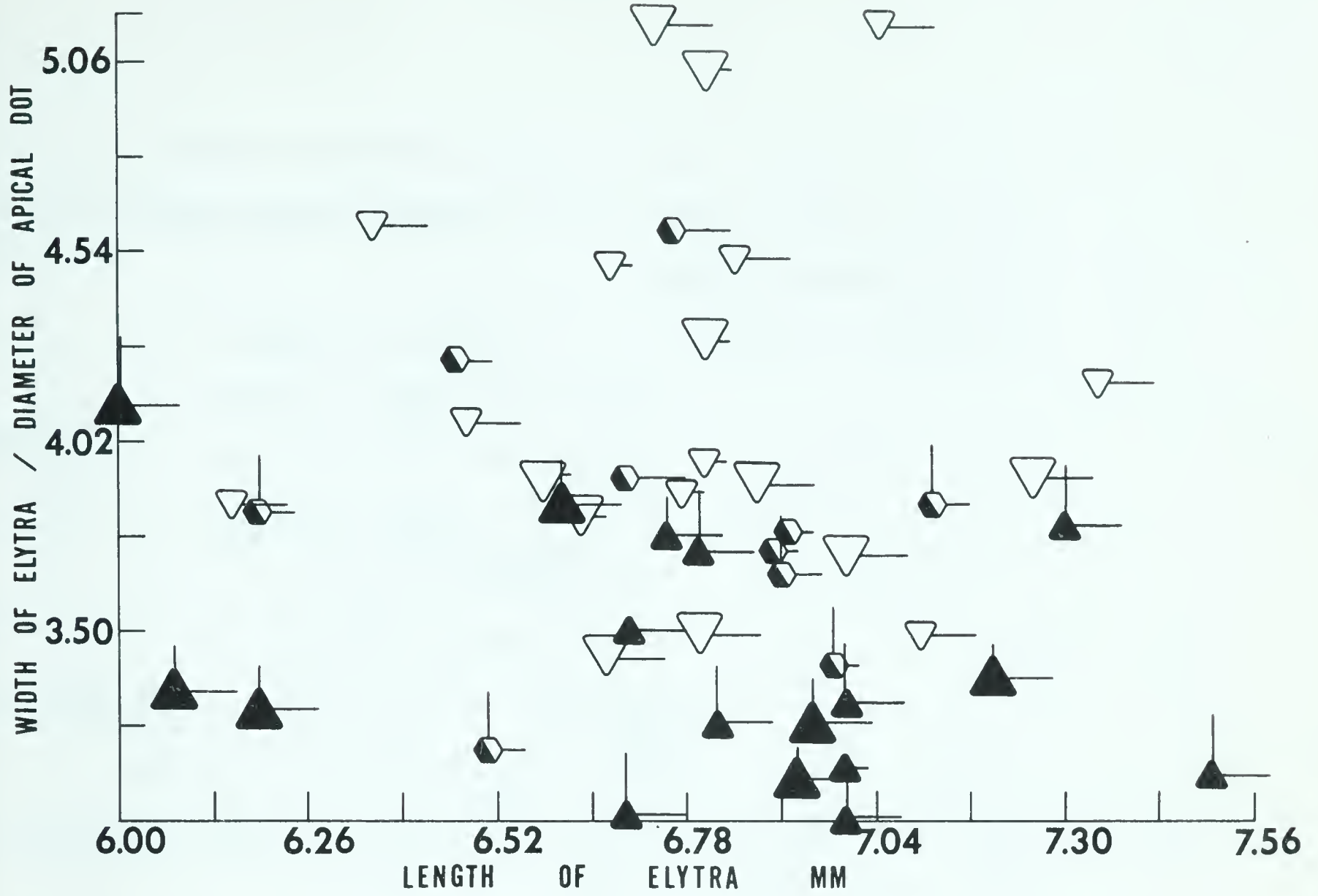




FIG. 24 - Pictorialized scatter diagram illustrating character differences between population samples of male Cicindela oregona guttifera and male Cicindela oregona maricopa.

Explanation of symbols: Squares - oregona guttifera.

Large - Fort Bridger, Wyoming

Small - Piute Reservoir, Utah

Black Triangles - oregona maricopa

Large - Caliente, Nevada

Small - Prescott, Arizona

Hexagons - specimens from an intermediate population
- Zion National Park, Utah

Vertical bar - color of elytra. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

Horizontal bar - color of thoracic pleura. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

FIG. 25 - Pictorialized scatter diagram illustrating character differences between sample populations of female Cicindela oregona guttifera and female Cicindela oregona maricopa.

Explanation of symbols: same as for FIG. 24.

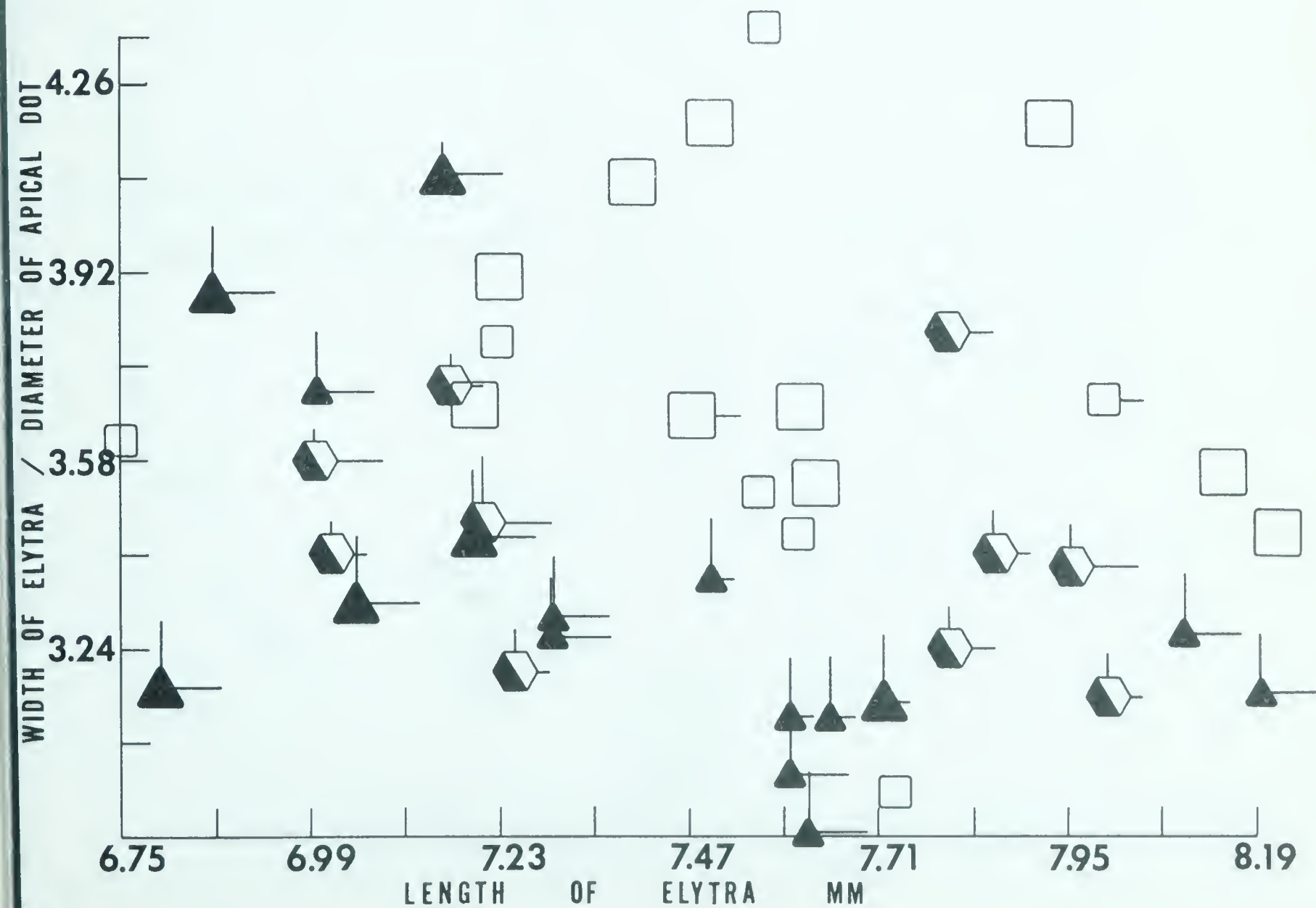
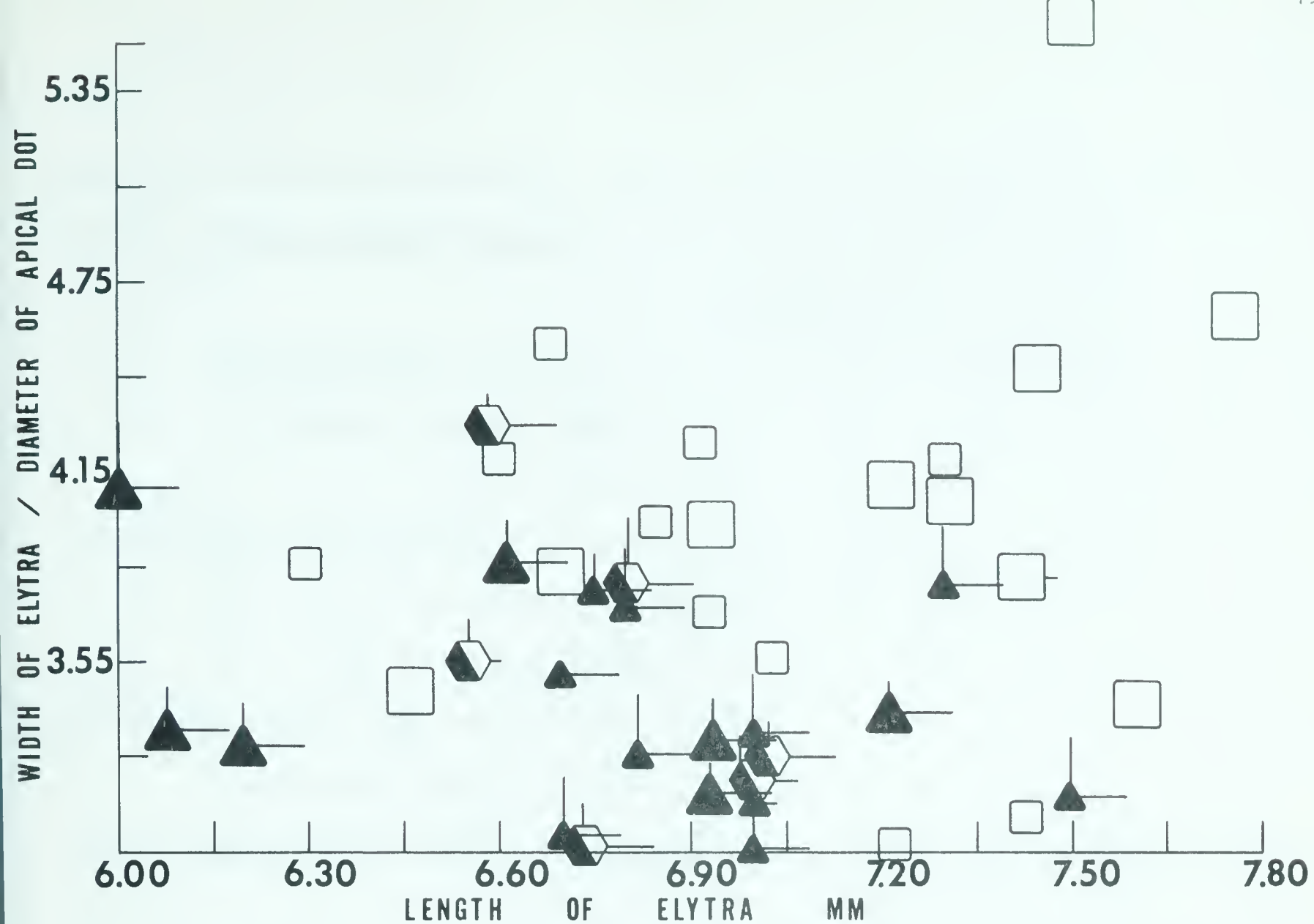


FIG. 26 - Pictorialized scatter diagram illustrating character differences between population samples of male Cicindela oregona guttifera and male Cicindela oregona navajoensis.

Explanation of symbols: Squares - Cicindela oregona guttifera

Small - Jemez Springs, New Mexico

Large - Vernal, Utah

Black circles - Cicindela oregona navajoensis

Small - Floy, Utah

Large - Kayenta, Arizona

Hexagons - specimens of an intermediate population
- Fort Wingate, New Mexico

Vertical bar - color of elytra. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

Horizontal bar - color of thoracic pleura. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

FIG. 27 - Pictorialized scatter diagram illustrating character differences between sample populations of female Cicindela oregona guttifera and female Cicindela oregona navajoensis.

Explanation of symbols: same as for FIG. 26.

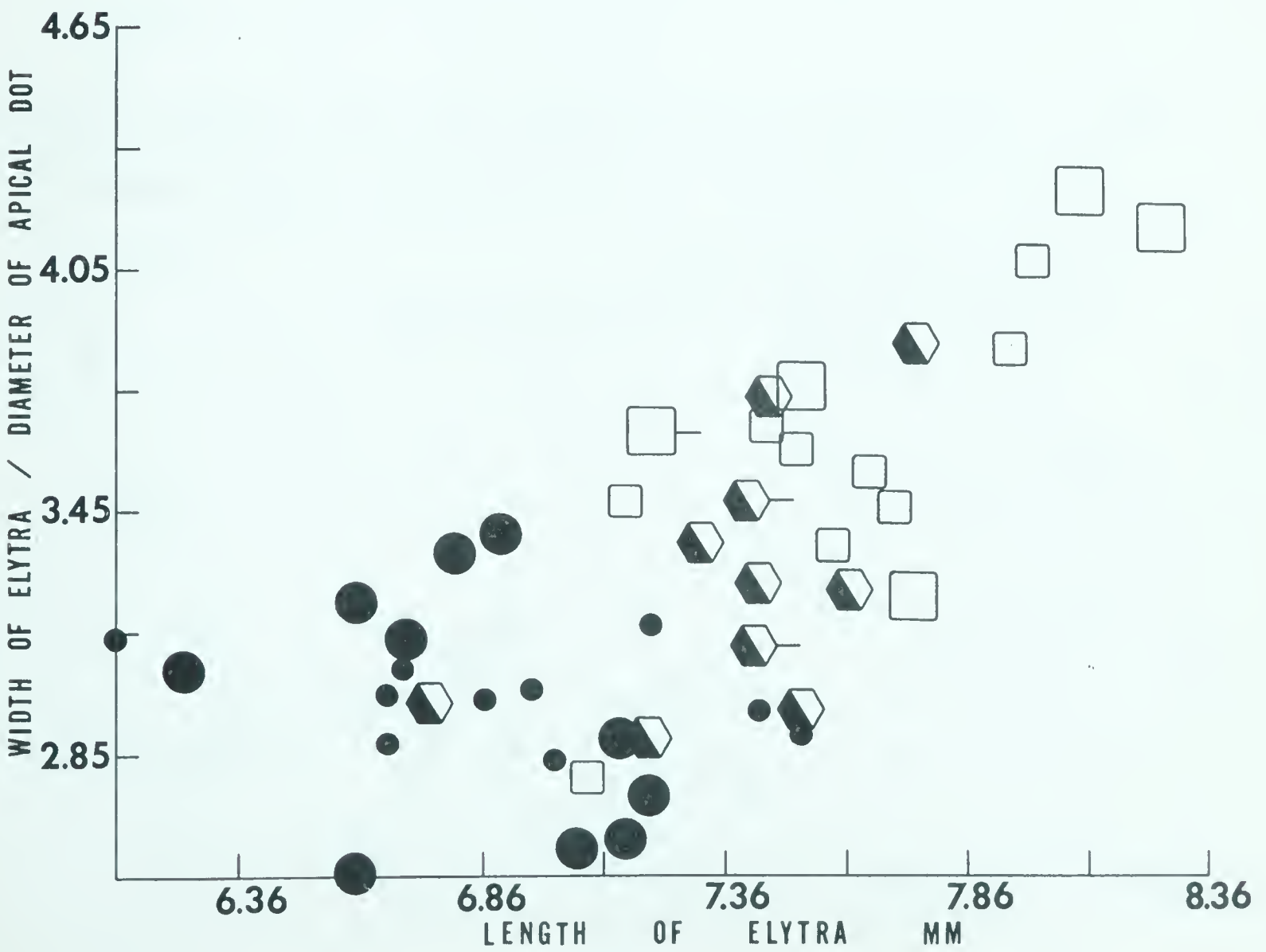
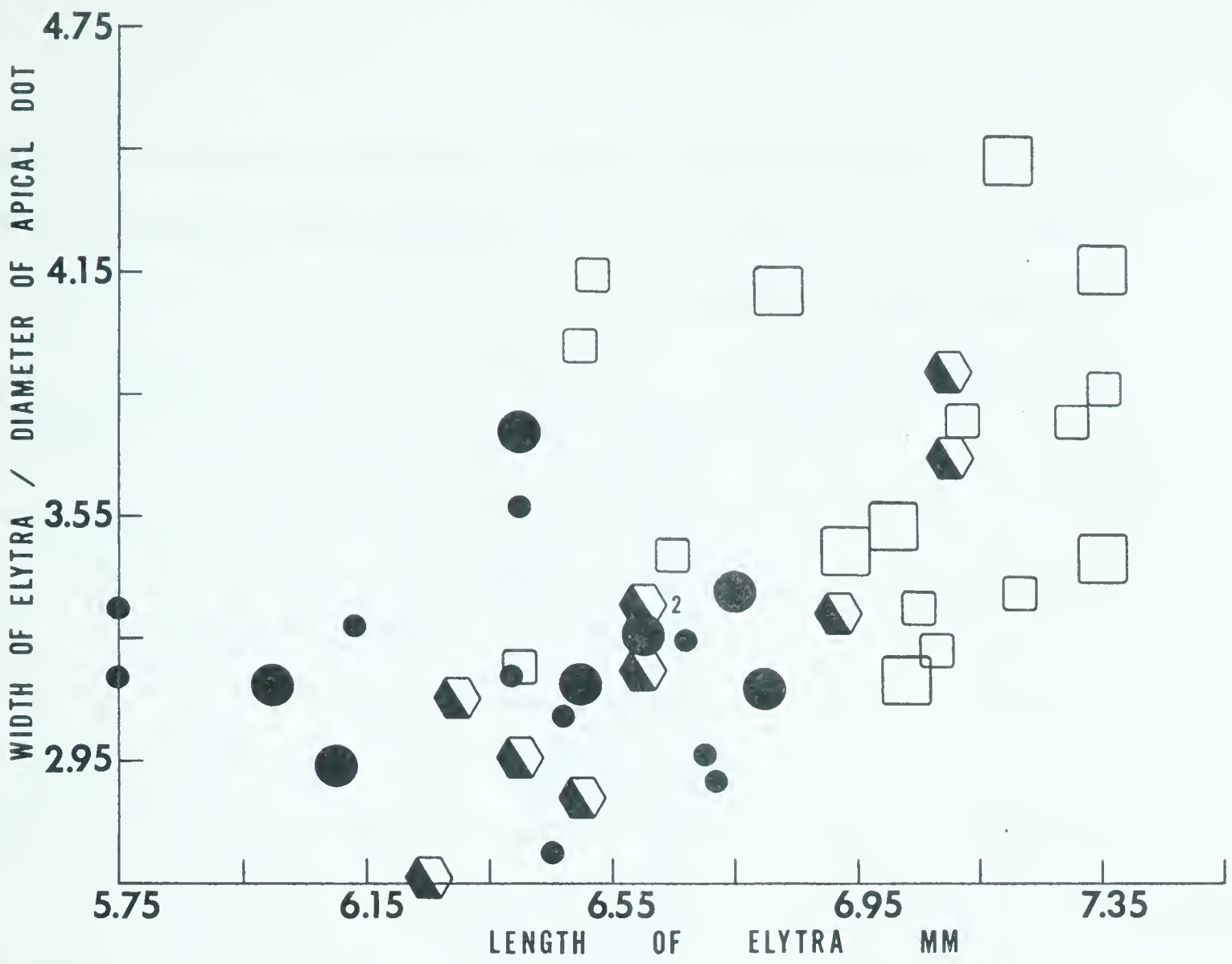


FIG. 28 - Pictorialized scatter diagram illustrating character differences between population samples of male Cicindela oregona oregona and male Cicindela oregona navajoensis.

Explanation of symbols: Inverted triangles - oregona oregona

Large - Yellowstone National Park, Wyoming

Medium - Owyhee County, Idaho

Small - Walker Lake, Nevada

Black circles - oregona navajoensis

Large - Kayenta, Arizona

Small - Floy, Utah

Vertical bar - color of elytra. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

Horizontal bar - color of thoracic pleura. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

FIG. 29 - Pictorialized scatter diagram illustrating character differences between sample populations of female Cicindela oregona oregona and female Cicindela oregona navajoensis.

Explanation of symbols: same as for FIG. 28.

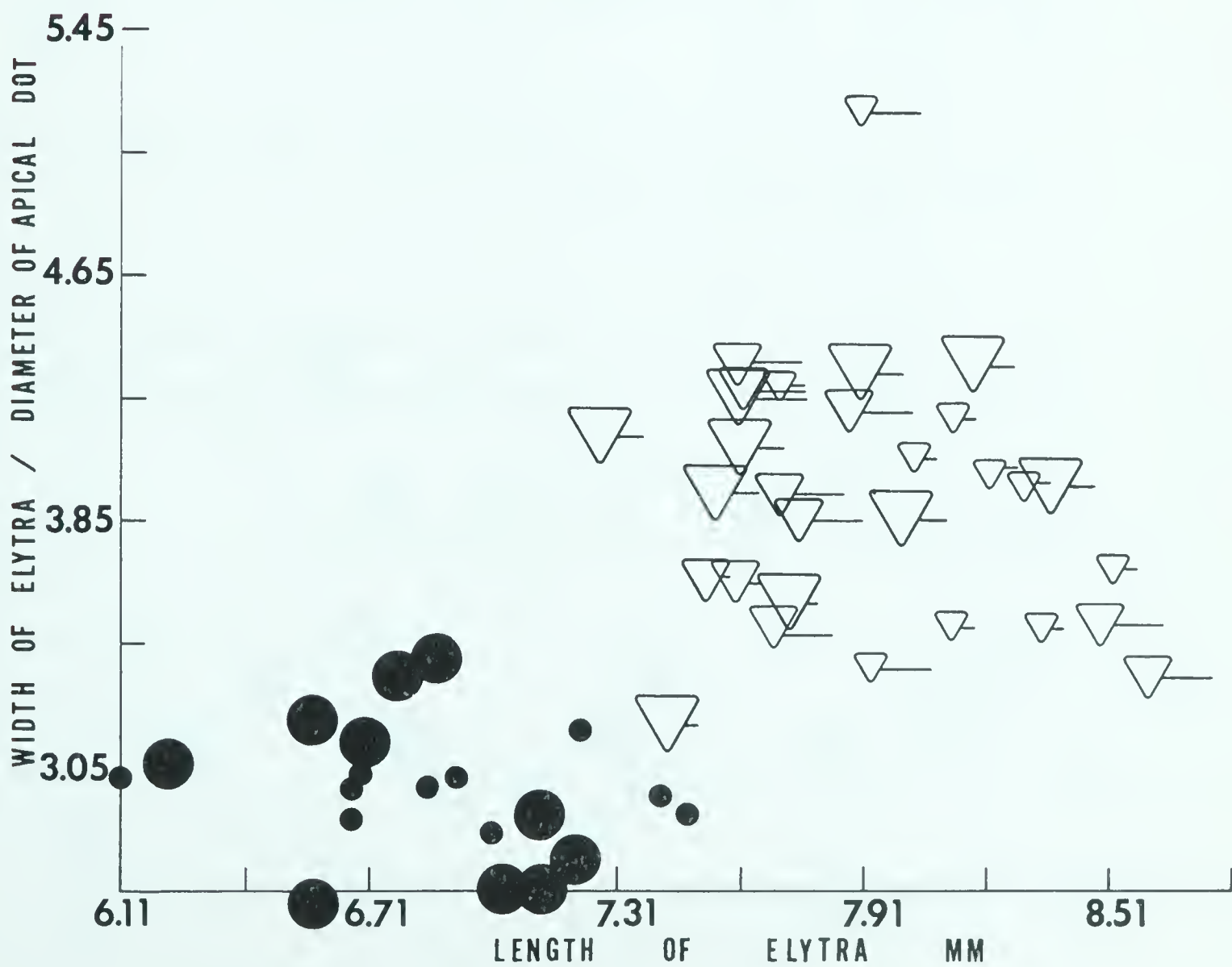
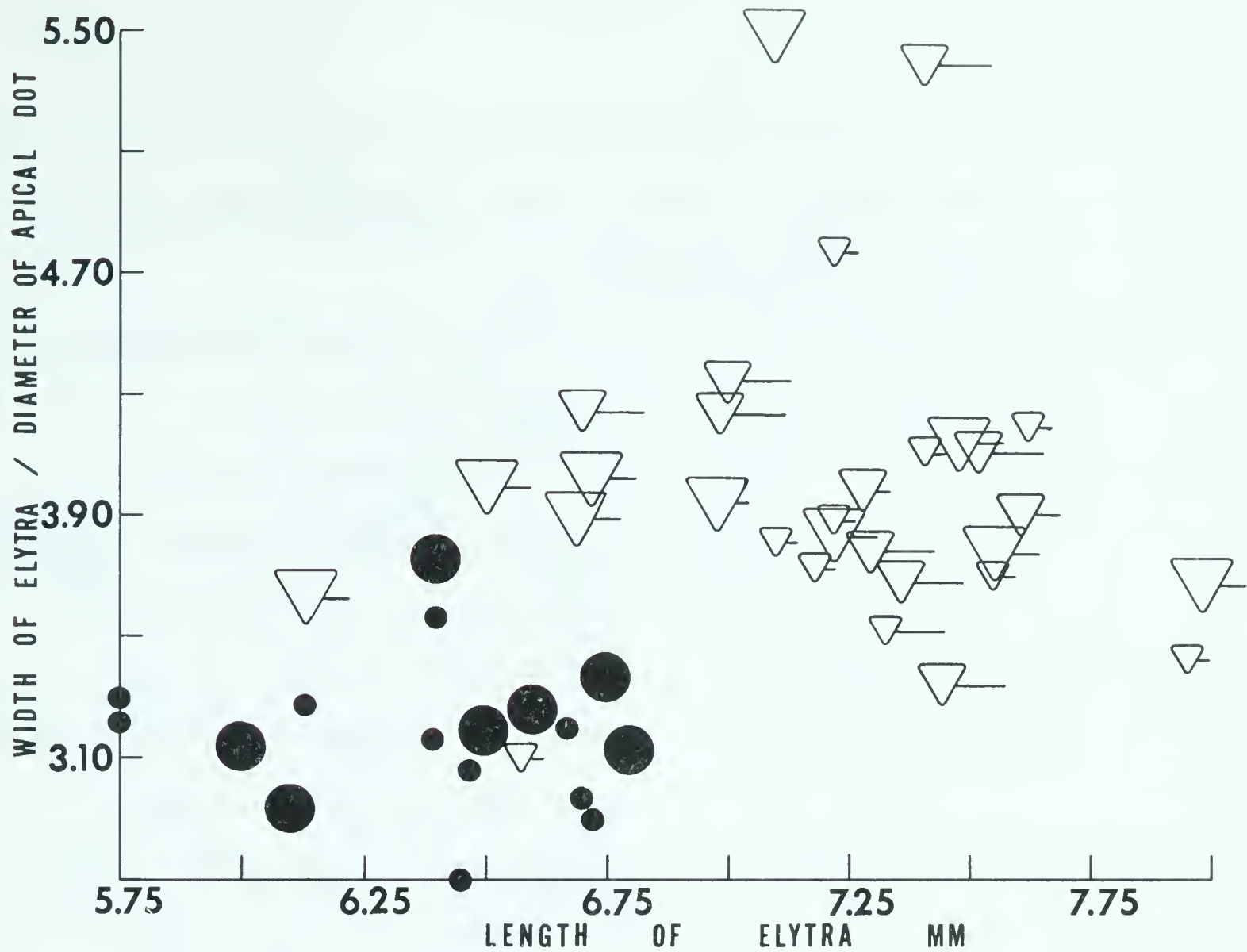


FIG. 30 - Pictorialized scatter diagram illustrating character differences between population samples of male Cicindela oregona maricopa and male Cicindela oregona navajoensis.

Explanation of symbols: Black circles - Cicindela oregona navajoensis

Large - Kayenta, Arizona

Small - Fort Wingate, New Mexico

Triangles - Cicindela oregona maricopa

Large - Mountain Park, New Mexico

Small - Globe, Arizona

Hexagons - specimens of intermediate populations

Large - Silver City, New Mexico

Medium - Carrizo, Arizona

Small - White Mountains, Arizona

Vertical bar - color of elytra. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

Horizontal bar - color of thoracic pleura. 6 mm - purple; 3 mm - green; 1.5 mm - blue; no bar - brown.

FIG. 31 - Pictorialized scatter diagram illustrating character differences between sample populations of female Cicindela oregona maricopa and female Cicindela oregona navajoensis.

Explanation of symbols: same as for FIG. 30.

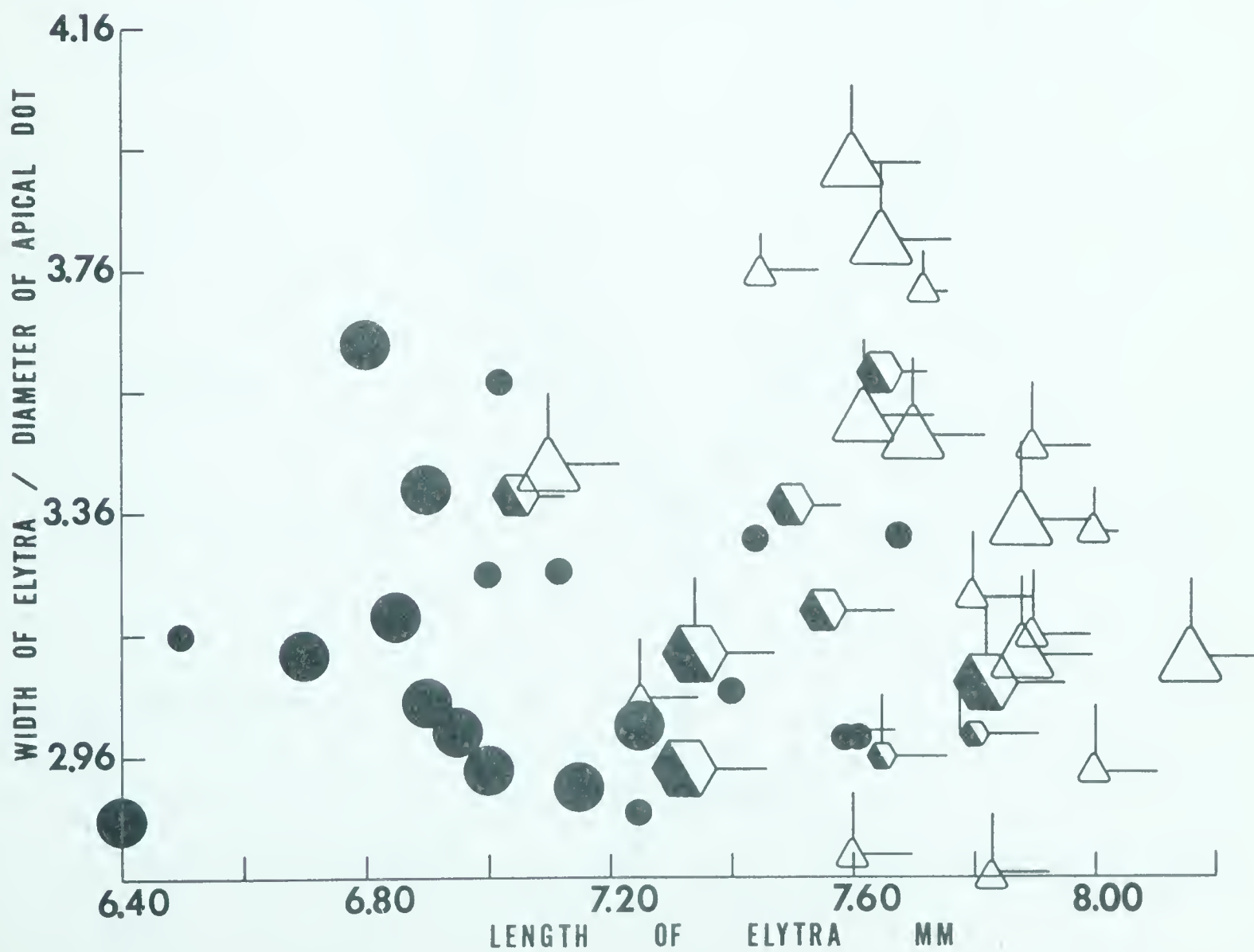
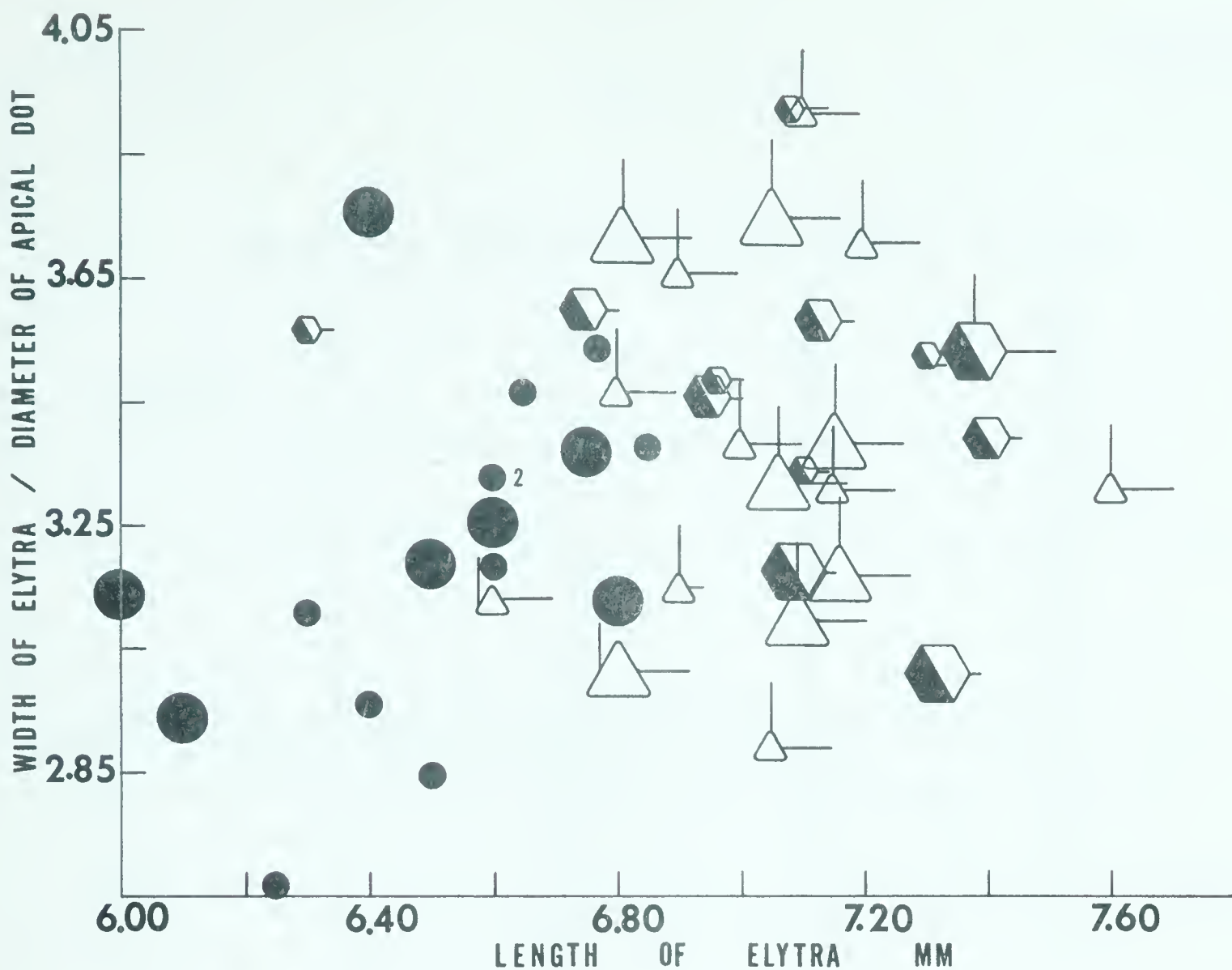


FIG. 32 - Hypothetical phylogeny of Cicindela oregona subspecies. The diagram is based on Pleistocene chronology postulated by Thor N.V. Karlstrom (1961).

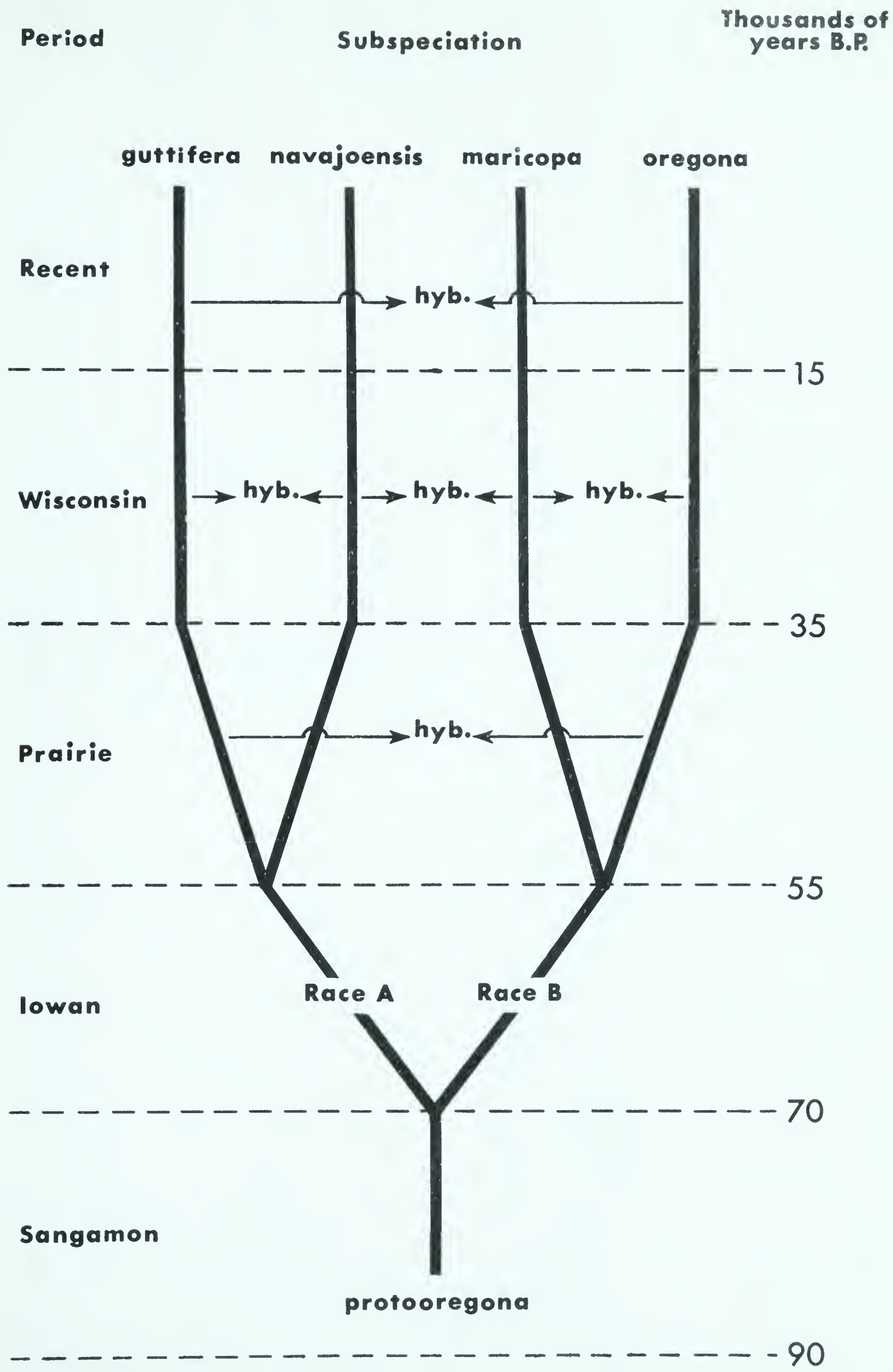


FIG. 33 - Geographical distribution of Cicindela depressula depressula
and Cicindela depressula eureka.

C. d. depressula - black dot.

C. d. eureka - black dot in white circle.

Specimens phenotypically eureka and depressula occur together if their symbols are linked. One symbol may represent a population or one specimen.

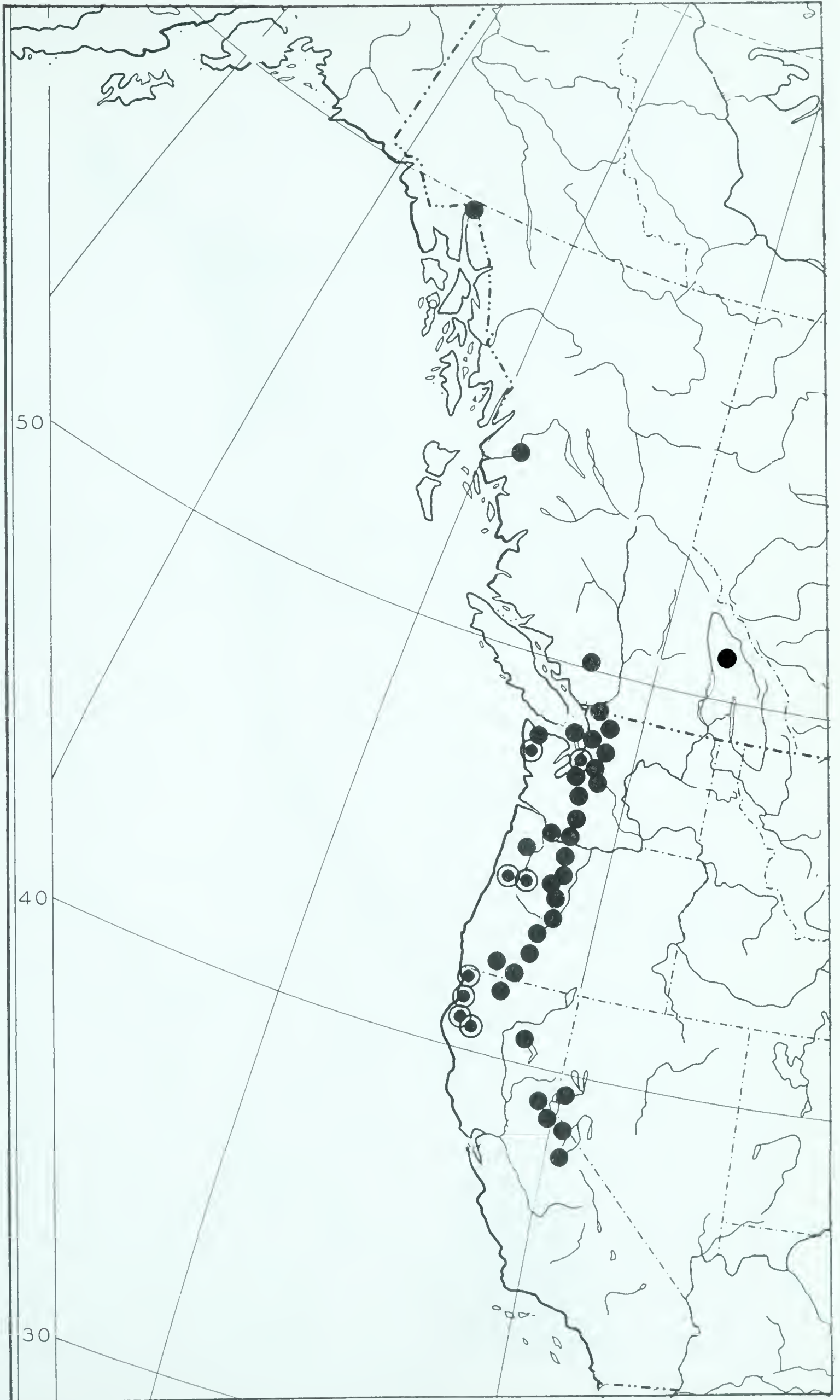


FIG. 34 - Locality map of population samples analysed by hybrid index method. Dark areas indicate elevations above 5,000 feet.

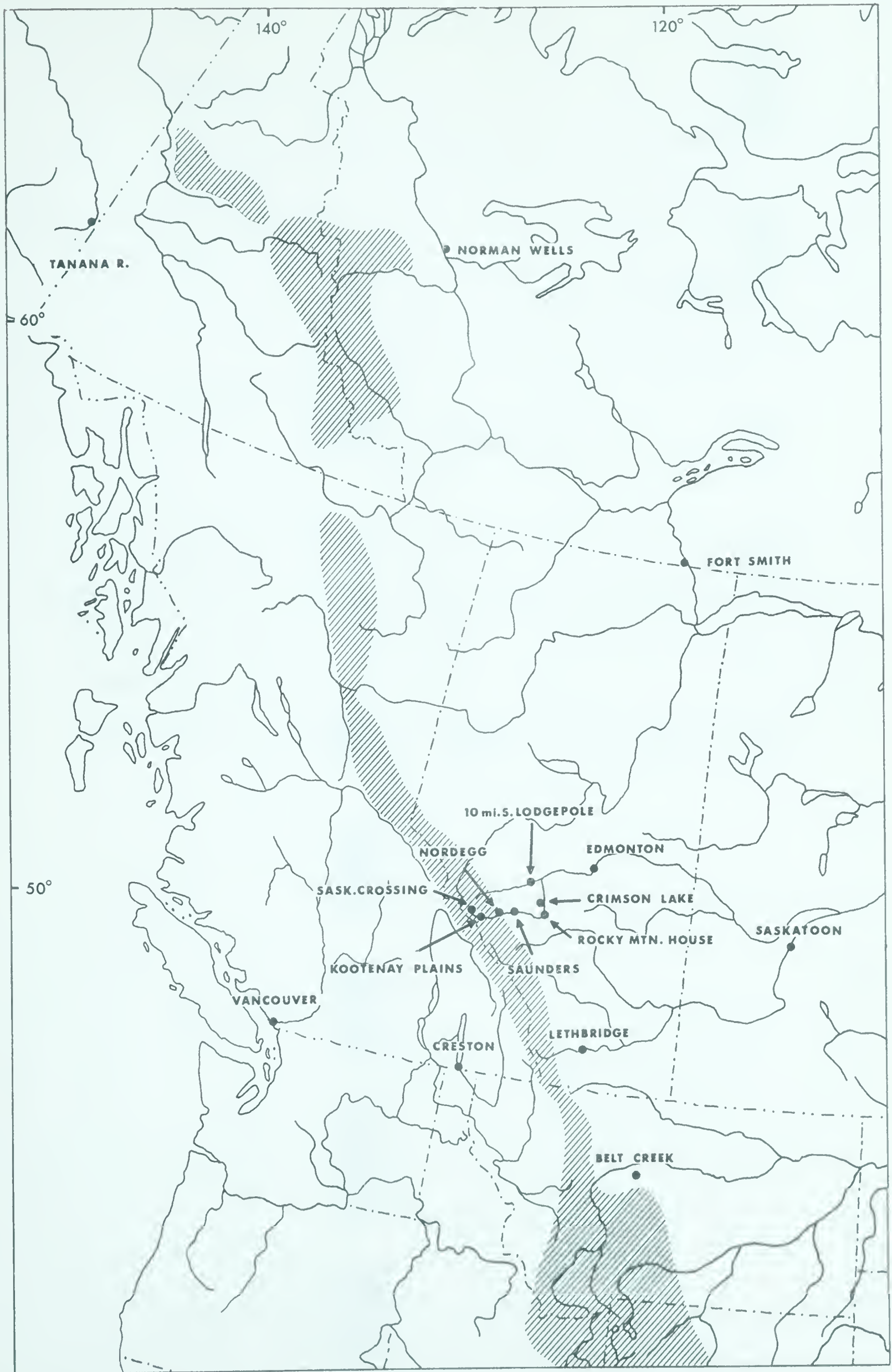


FIG. 35 - Histograms of some population samples collected in western Canada. Average hybrid indices and the change in hybrid index units per mile are indicated on the right side of the figure. Number of specimens per sample and air miles between localities from which population samples were collected are indicated on the left side.

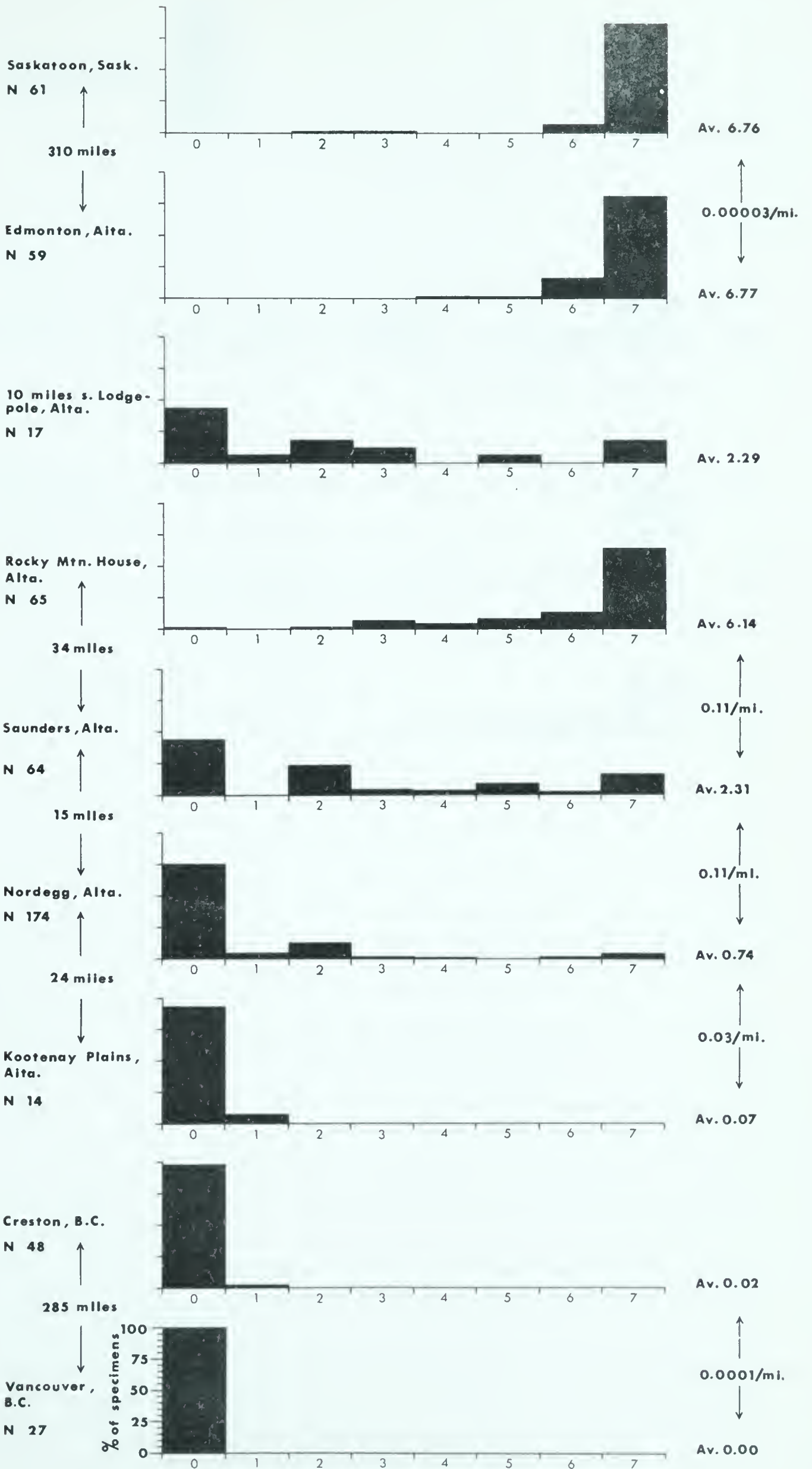
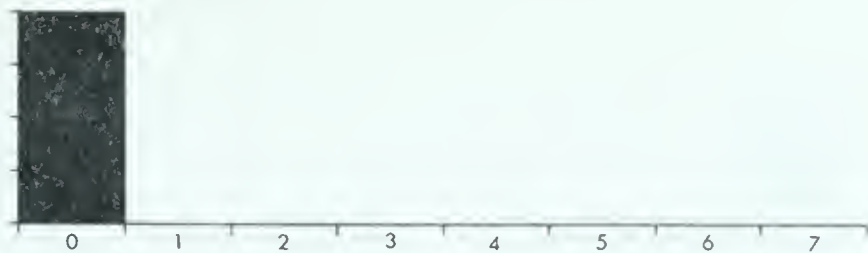


FIG. 36 - Histogram of a hybrid population sample from Saskatchewan
Crossing, Alberta.

FIG. 37 - Histogram of a hybrid population sample from Garth, Alberta.

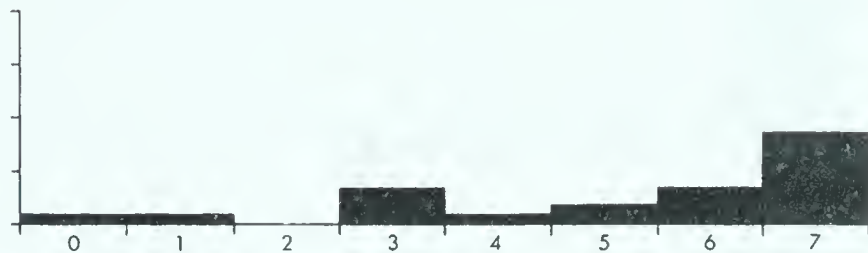
FIG. 38 - Histograms of some hybrid population samples from Rocky
Mountain House, Alberta.

North Sask. R. Alta.
nr. Sask. Crossing
N 10



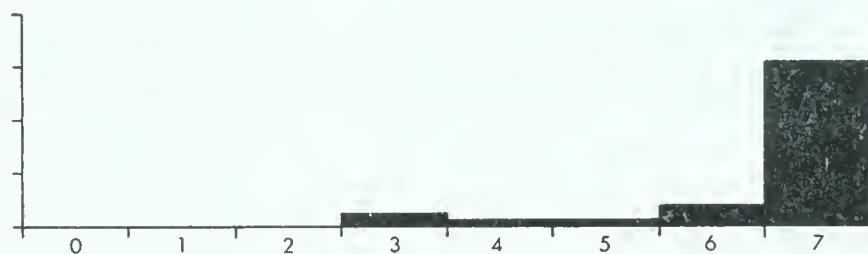
Av. 0.00

Garth, Alta. May,
1963
N 23



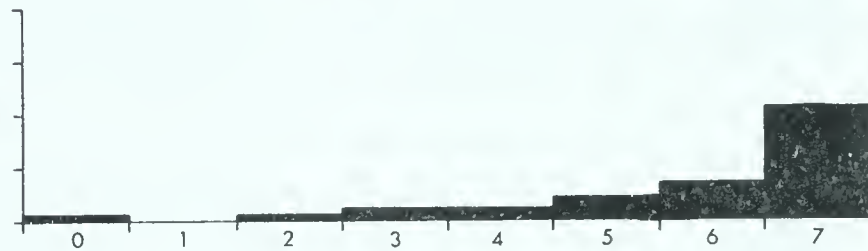
Av. 5.25

Rocky Mtn. House,
Alta. May, 1963
N 31



Av. 6.49

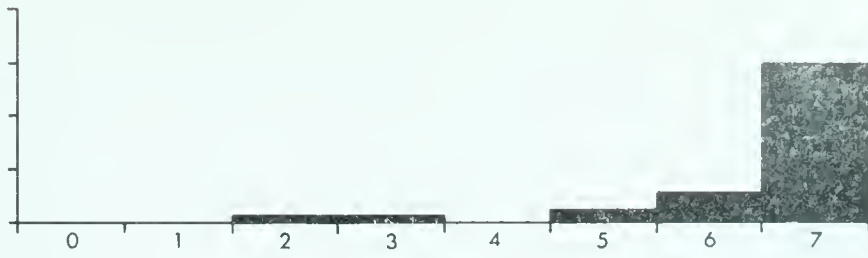
Rocky Mtn. House,
Alta. Aug., 1963
N 34



Av. 5.83

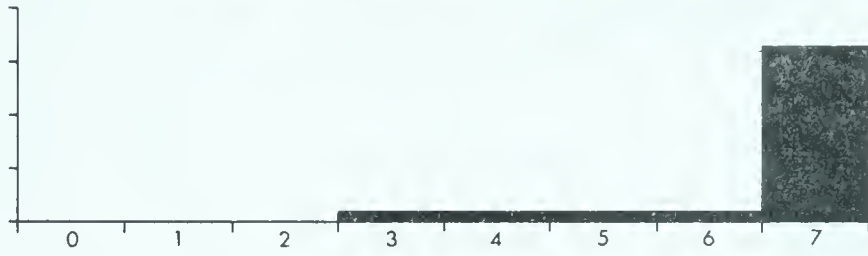
FIG. 39 - Histograms of some hybrid population samples from Crimson
Lake, Alberta.

Crimson Lake, Alta.
1961
N 36



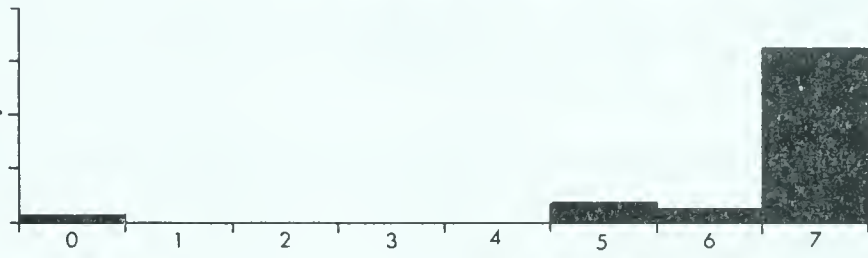
Av. 6.50

Crimson Lake, Alta.
1962
N 65



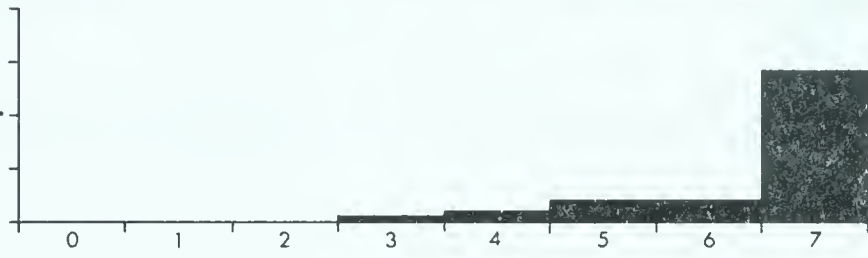
Av. 6.53

Crimson Lake, Alta.
May, 1963
N 33



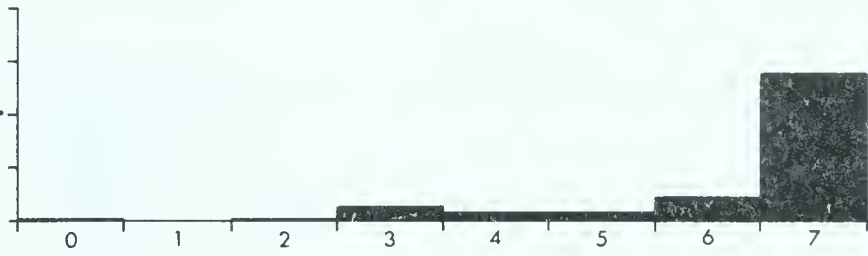
Av. 6.55

Crimson Lake, Alta.
July, 1963
N 38



Av. 6.43

Crimson Lake, Alta.
August, 1963
N 45



Av. 6.14

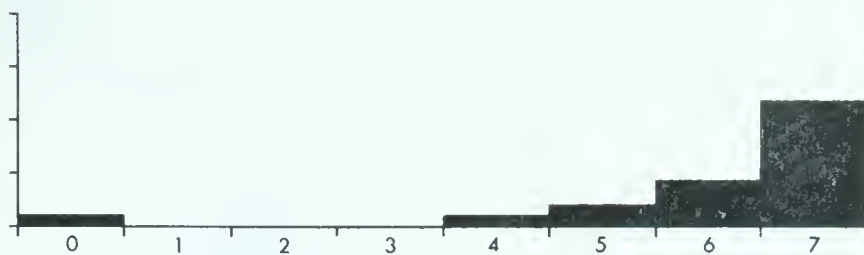
FIG. 40 - Histograms of some hybrid population samples from eight miles south of Lodgepole, Alberta.

FIG. 41 - Histogram of a hybrid population sample from Lethbridge, Alberta.

FIG. 42 - Histogram of a hybrid population sample from Belt Creek near Armington, Montana.

8 miles s. Lodge -
pole, Alto. July,
1963

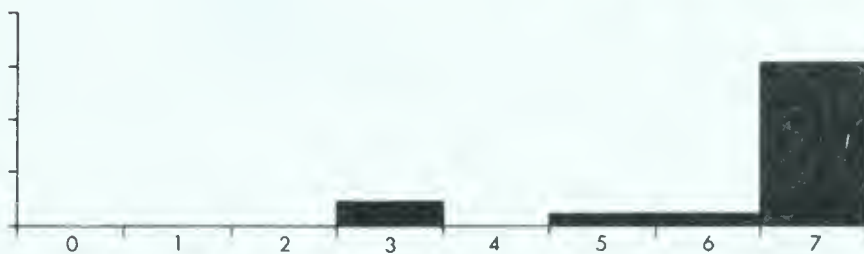
N 19



Av. 6.06

8 miles s. Lodge -
pole, Alto. August,
1963

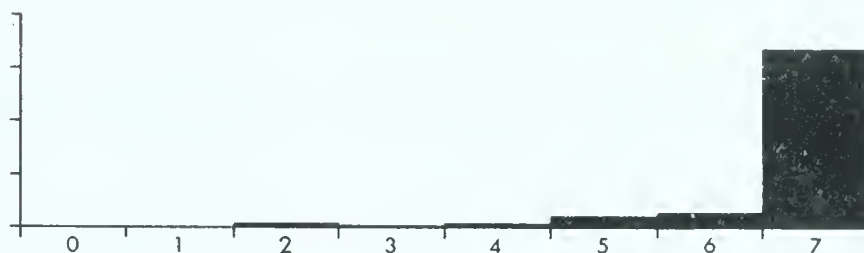
N 17



Av. 6.36

Lethbridge, Alto.
1962

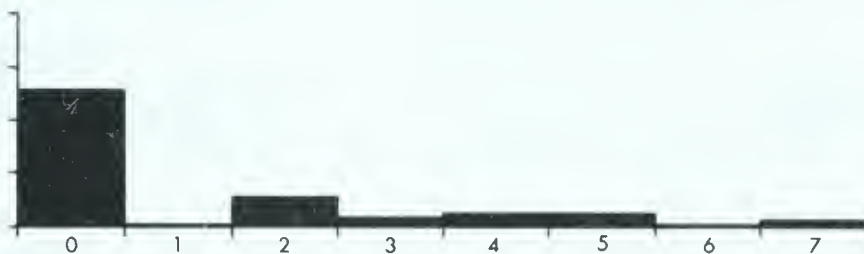
N 310



Av. 6.66

Belt Ck. e. Arming-
ton, Mont. 1963

N 70



Av. 1.23

FIG. 43 - Histograms of some hybrid population samples from Alaska and the Northwest Territories.

FIG. 44 - Histograms of some hybrid population samples from Nordegg, Alberta.

Tanana R., Mi. 1281
Alas. Hway. Alas.

N 27

470 miles

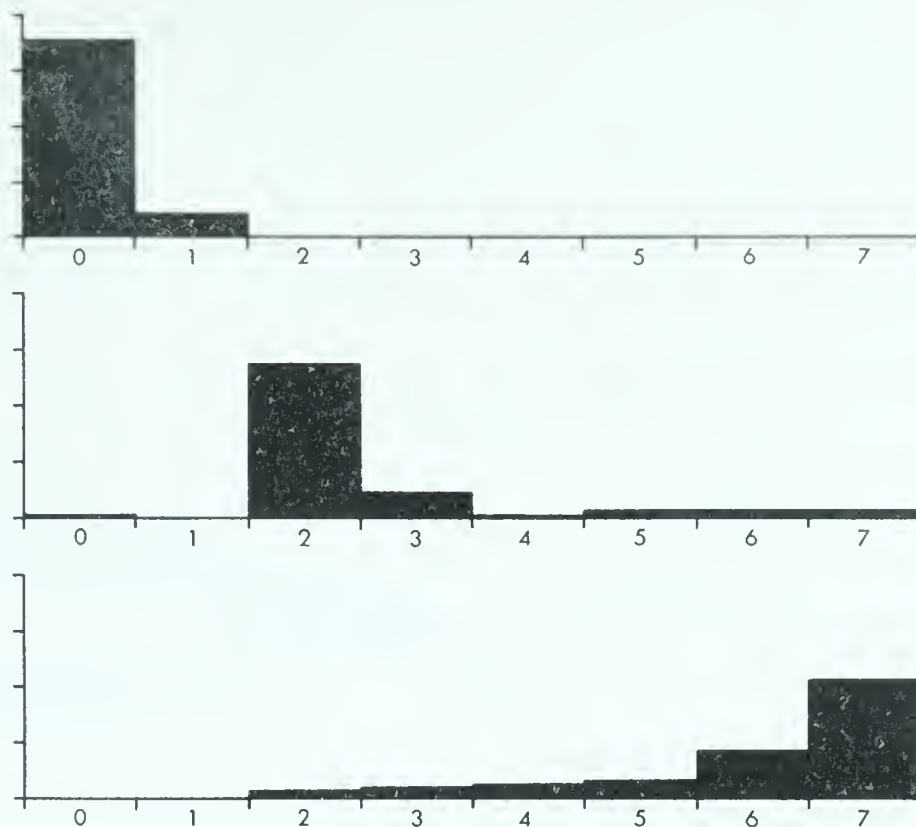
Norman Wells,
N.W.T.

N 43

580 miles

Fort Smith, N.W.T.

N 162



Av. 0.11

0.00547/mi.

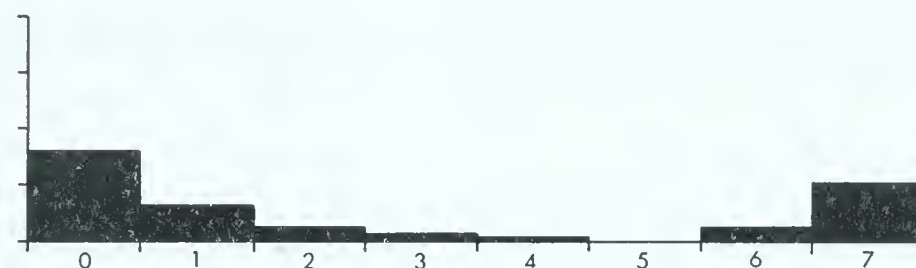
Av. 2.68

0.00567/mi.

Av. 5.97

Nordegg, Alta. 1961

N 83



Av. 2.60

Nordegg, Alta. 1962

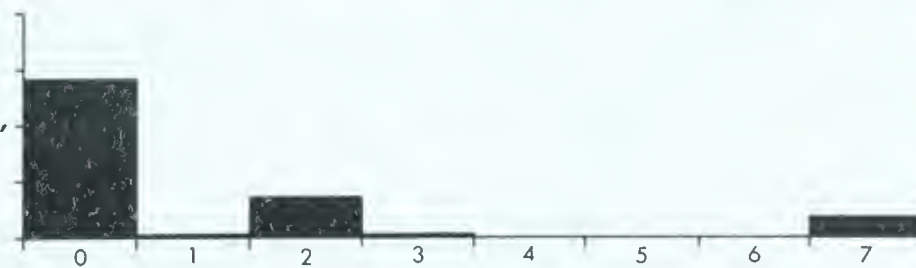
N 219



Av. 0.97

Nordegg, Alta. May, 1963

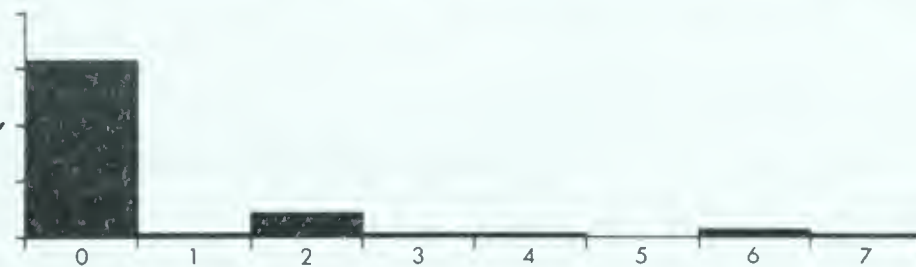
N 62



Av. 0.98

Nordegg, Alta. July, 1963

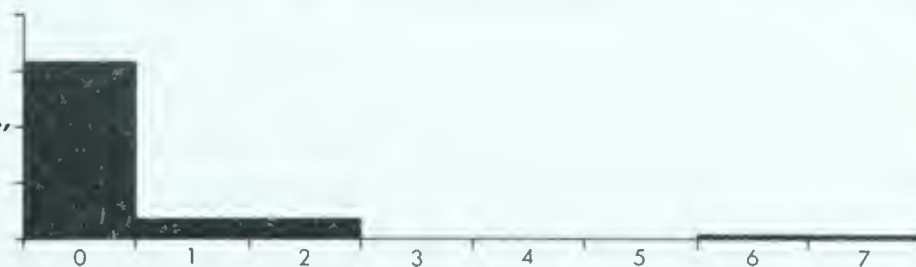
N 54



Av. 0.72

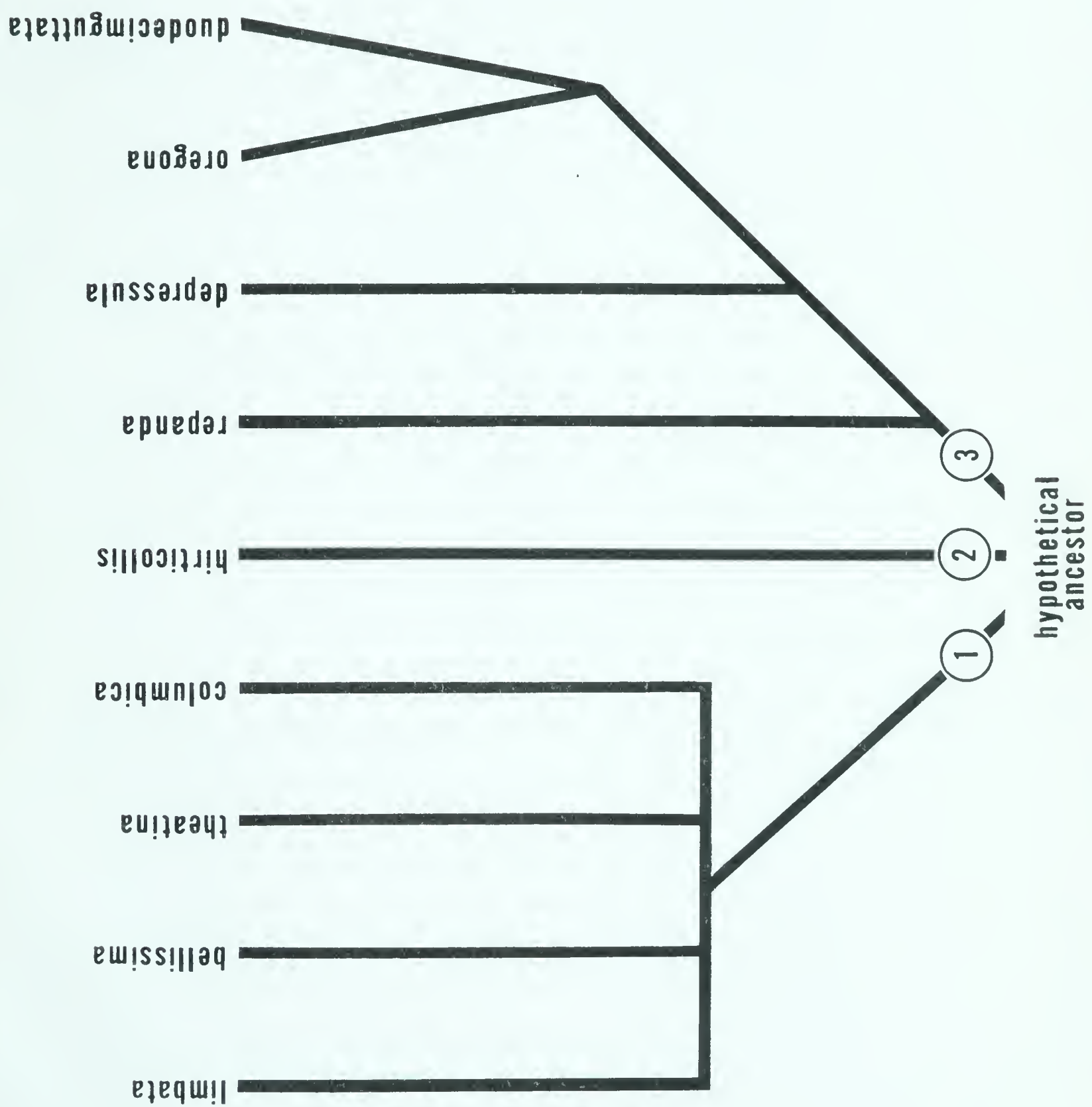
Nordegg, Alta. Aug., 1963

N 58



Av. 0.48

FIG. 45 - Hypothetical phylogeny of the North American
species of the maritima group.



B29828